Vol. LIV No. 5

THE BOTANICAL GAZETTE

November 1912

Editor: JOHN M. COULTER

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The University of Chicago Press
CHICAGO, ILLINOIS

Agents
THE CAMBRIDGE UNIVERSITY PRESS, *London and Edinburgh*
WILLIAM WESLEY & SON, *London*
TH. STAUFFER, *Leipzig*
THE MARUZEN-KABUSHIKI-KAISHA, *Tokyo, Osaka, Kyoto*

The Botanical Gazette

A Monthly Journal Embracing all Departments of Botanical Science

Edited by JOHN M. COULTER, with the assistance of other members of the botanical staff of the University of Chicago.

Issued November 13, 1912

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The Botanical Gazette is published monthly. ¶The subscription price is $7.00 per year; the price of single copies is 75 cents. ¶Postage is prepaid by the publishers on all orders from the United States, Mexico, Cuba, Porto Rico, Panama Canal Zone, Republic of Panama, Hawaiian Islands, Philippine Islands, Guam, Tutuila (Samoa), Shanghai. ¶Postage is charged extra as follows: For Canada, 35 cents on annual subscriptions (total $7.35), on single copies, 3 cents (total 78 cents); for all other countries in the Postal Union, 84 cents on annual subscriptions (total $7.84), on single copies, 11 cents (total 86 cents). ¶Remittances should be made payable to The University of Chicago Press, and should be in Chicago or New York exchange, postal or express money order. If local check is used, 10 cents must be added for collection.

The following agents have been appointed and are authorized to quote the prices indicated:

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Business correspondence should be addressed to The University of Chicago Press, Chicago, Ill.

Communications for the editor should be addressed to him at The University of Chicago, Chicago, Ill.

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Illustrations are furnished without cost to author only when suitable originals are supplied. A copy of the suggestions made in the January number, 1907, will be sent on application. It is advisable to confer with the editors as to illustrations required in any article to be offered.

Separates, if desired, must be ordered in advance of publication. Twenty-five separates of original articles without covers will be supplied gratis. A table showing approximate cost of additional separates is printed on an order blank which accompanies the proof; a copy will be sent on request.

Entered August 21, 1896, at the Post-office at Chicago, as second-class matter, under Act of Congress March 3, 1879.

VOLUME LIV NUMBER 5

THE
BOTANICAL GAZETTE

NOVEMBER 1912

THE DEVELOPMENT OF BLASTOCLADIA STRANGULATA, N. SP.[1]

J. T. BARRETT

(WITH PLATES XVIII–XX)

The genus *Blastocladia* was founded and incompletely described in 1876 by REINSCH (**6**) on the single species *B. Pringsheimii*, which for twenty years remained its sole representative. In 1896 THAXTER (**9**) rediscovered and made a careful study of the plant, which up to that time, apparently, had not been again observed. His studies cleared up several doubtful or unknown points in connection with its life-history and development, and led to the description of a new species, *B. ramosa*. Up to the present, so far as the writer is aware, no other species has been added to the genus. Aside from its peculiar characters, the genus is of particular interest because of its doubtful systematic position. Because of the resemblance of the resting spores to the deciduous conidia of certain *Pythium* species, THAXTER (**9**) placed the genus provisionally among the Pythiaceae. FISCHER (**1**) considers it with the genera which are doubtful or to be excluded from the Saprolegniaceae, while SCHRÖTER (**7**) includes it with the Leptomitaceae.

The species described in this paper fixes with considerable certainty, the writer believes, the true systematic position of the genus and is therefore described in detail.

This study was undertaken in the Botanical Laboratory of Cornell University under the supervision of Professor GEORGE F.

[1] Contribution from the Department of Botany, Cornell University. No. 140.

ATKINSON, to whom I wish to express my thanks for his advice and kindly criticisms.

Material and methods

A single plant of this species was discovered growing on an aphid which had accidentally fallen into one of several water cultures prepared for the purpose of entrapping various Phycomycetes. The specific culture referred to was made from soil and decaying vegetation taken from the bottom of a small almost dry inland pond in the vicinity of Ithaca. When first observed the plant bore large numbers of resting sporangia, whose arrangement and bright orange color gave it a very beautiful appearance. After washing through several changes of sterile water, the plant was placed in a solid watch glass for further observation. On examination the following day it was found that a number of zoosporangia had developed, a few of which had already discharged the characteristic zoospores first described by THAXTER (9) for *B. Pringsheimii.*

Cultures were immediately started with aphids and other animal tissue, from which an abundance of material in all stages of development was secured. After making several unsuccessful attempts, a pure culture of the organism was obtained in the following manner: A few nearly mature zoosporangia were cut from a plant, carefully washed until practically free from contamination, and allowed to discharge their zoospores in sterile water. By means of a platinum loop the water containing the zoospores was spread over the surface of newly prepared slants of sweet corn agar. In a few days the small plants appeared as more or less isolated refractive specks on the surface of the agar, and were easily lifted out with a sterile needle and transferred to new tubes.

Material for sectioning was obtained in various stages of development from both water and agar cultures. It was soon found that the latter yielded just as good and more easily handled material than the former and it was therefore more frequently used. To secure the best results with the latter method, plants bearing nearly mature zoosporangia were transferred to the middle of a poured plate of either potato or sweet corn agar, preferably the latter, in a few drops of sterile water. After a few hours to one day large numbers of zoospores will have been discharged and can easily be

spread over the plate by rocking the same or by the use of a sterile platinum loop. Thus distributed, the zoospores soon germinate and produce large numbers of usually simple plants bearing the reproductive organs. They commonly lie sufficiently close so that most of the agar may be cut out and fixed for microscopic study.

Three different killing solutions were used, which gave various results. These were medium chrom-acetic acid, Flemming's weak solution, and Gilson's fixer. After dehydration in the grades of alcohol or by evaporating down from 10 per cent glycerine, the material was cleared in cedar oil and imbedded in paraffin. Sections were cut 2–5 μ thick and stained on the slide.

The stains used were Flemming's triple stain with the orange G dissolved in clove oil, Heidenhain's iron-alum hematoxylin, and Gram's stain. The triple stain following Flemming's weak solution gave the best material for the study of the walls of the resting sporangia, papillae of dehiscence, and for fragmentation of the protoplasm to form zoospores; while Heidenhain's hematoxylin, when preceded by medium chrom-acetic acid, gave much the best material for the study of the protoplasm and nuclei. Gram's stain proved very good as a nuclear stain.

Description of the plant

The plant consists of a basal cell or cylinder whose lower extremity is attached to the substratum by a system of rhizoids, and supports above a dichotomously or umbellately branched system whose final branchlets terminate in one or more reproductive bodies (figs. 12, 58). At the points of origin of the branches, and occasionally elsewhere, there are more or less well marked constrictions of the mycelium. This character at once suggests a relationship to the members of the Leptomitaceae. The constrictions, however, are more abrupt and usually of less depth than those of that family. They mark off the plant into definite segments which are fairly constant in diameter throughout, although they occasionally have a tendency to enlarge slightly at one or both ends. This is especially noticeable in those branches which give rise to more than two branchlets. In this they resemble somewhat the branchlets of *Rhipidium americanum* Thaxter (10).

At the constricted points one finds pseudo-septa in various stages of development. These peculiar structures are unlike anything in the way of septa that I have seen described. In the older parts of the plant they reach their most perfect development, and then only incompletely separate the protoplasm of the adjacent segments. In a single well developed plant of some age, one may find the pseudo-septa in all stages of formation. They are first seen as separate processes or thickenings protruding inwardly from the wall at the constrictions. These processes increase in length, probably by accretion, until on meeting at the center of the cell, a fusion takes place and a definite central plate results.

Fig. 18, *a–d*, represents different stages of development of a septum, while figs. 19, 20, and 21 represent sections through such a stage as that shown in fig. 18, *a*. In fig. 19 the section is through one arm and the central plate, fig. 20 through two opposite radial arms and the central plate, while fig. 21 shows a section through the central plate alone. These pseudo-septa are much more highly differentiated than the "cellulin" rings which are present in *Gonapodya* and other Leptomitaceae. They permit a free interchange of the protoplasm, and only under conditions of injury to the hypha do they entirely close the lumen. Both the mycelial walls and the pseudo-septa fail to give any definite reaction for cellulose. After treatment with iodine and sulphuric acid, very rarely a slight trace of blue color is seen in the mycelial walls. The pseudo-septa become much swollen and take on a deep orange color, resembling in this respect the reaction secured by PRINGSHEIM (**5**) for the "cellulin granules."

In young actively growing plants the protoplasm is much vacuolated, granular, and contains, distributed throughout it, prominent nuclei containing deeply staining bodies (figs. 28, 32). Aside from the nuclei, there occur other deeply staining bodies which are more or less regular in form and of various sizes. They are very probably similar to those described by REINSCH (**6**) as independent, endogenously produced cells, which he was inclined to believe were the origin of the reproductive organs (see figs. 12, 28, 32). THAXTER (**9**) observed these same bodies in *B. Pringsheimii*, and saw no reason for assuming that they were other than

masses of fatty protoplasm. Their true nature has not been determined, but, as will be shown later, they have at least one definite function in connection with zoospore formation. They are always present in more or less abundance, their extent of occurrence depending, to a degree at least, on growth conditions of the plant. In old plants, especially when the production of reproductive bodies has ceased, large groups of such bodies may be seen collected near the pseudo-septa, and frequently elsewhere in the mycelium.

Bodies somewhat similar in appearance are known to occur in the hyphae of members of the Saprolegniaceae. PRINGSHEIM (5) describes these at length and records a series of microchemical tests to determine their nature. According to his conclusions they are neither a proteid nor a carbohydrate substance, but rather waste products of metabolism.

Under favorable conditions of growth, a branchlet when terminated by a reproductive body may continue its growth by the production of a sub-branch (fig. 32). This sub-branch may be likewise terminated, sooner or later, and continued growth repeated as before. The length and rapidity of growth of these sub-branches determines whether the reproductive bodies shall occur at intervals or in a more or less compact head or group (figs. 6, 7, 12). This type of sympodial branching occurs in depauperate specimens of *Rhipidium americanum* (THAXTER 10). It has also been noted for *Apodachlya*.

Under the best normal conditions for growth, the production of zoosporangia precedes that of resting sporangia. In pure cultures this order is easily reversed by properly manipulating external conditions. In a frequently refreshed culture, zoosporangia alone are at first produced, while on the other hand plants in a culture started and maintained in a small amount of water usually give rise to resting sporangia only.

The extent to which branching may proceed before the production of reproductive organs varies greatly. This may continue until a well formed almost hemispherical tuft is produced, or on the other hand zoosporangia may develop soon after the germination of the zoospore on the terminal end of the more or less

elongated basal cell. This condition occurs particularly on young plants started on agar and subsequently transferred to water. If sufficient moisture is present the same thing may take place directly on the agar (figs. 4, 5). Zoosporangia may be produced singly or in chains (fig. 59).

The growth of the plant is rapid when the best external conditions are offered. Observations made relative to this point showed that in one case hyphae which were just emerging from the body of an aphid at 10:30 A.M. had produced at 5:30 P.M. of the same day mature zoosporangia, some of which were discharging zoospores. The size of individual plants varies greatly with the purity of the cultures and the nature and amount of nutrient material at hand.

Development of zoosporangia

The zoosporangia are broadly oval to almost spherical, rarely elliptical, smooth, hyaline, and fairly constant in form and size. They may originate terminally or subterminally on the branchlets. In the former case the first indication of such a development is a slight swelling of the hyphal end accompanied by a well marked change in the protoplasm (fig. 11, *a–c*). Before reaching its normal size, the zoosporangium becomes cut off from the hypha by a septum, and papillae of dehiscence begin to appear. When produced subterminally, the mature zoosporangium may be borne on a more or less elongated branchlet, as previously noted, which originated from the parent branch directly below another reproductive body (fig. 6), may be sessile (fig. 12, *b*), or even develop as swollen segments cut off by septa (fig. 12, *a*). The latter method when continued produces a chain of zoosporangia (fig. 59). As a result of cutting off the ends of fertile branches, zoosporangia may bud out from the remaining parts in various places. In certain instances the contents of the injured branches give rise to zoospores without any modification in form.

The zoosporangia of *B. Pringsheimii*, after discharging their zoospores, drop from the plant, leaving numerous scars. This was noted by THAXTER (**9**) and also by PETERSEN (**4**). I have never observed this phenomenon to take place in *B. strangulata*. Old

empty zoosporangia may be seen still attached to the plants weeks after they have ceased to produce reproductive organs.

As growth of the zoosporangium proceeds, there is a noticeable condensation of the protoplasm in the center, around which can be seen a number of indistinct vacuoles of irregular shape. There is little apparent change from this condition until the zoosporangium has reached its maximum size. The contents then become coarsely granular and no vacuoles are apparent. This stage may persist for some time if conditions for further development become poor. In fact, it is in this stage that zoosporangia rest at times for days. Suddenly the coarse granular character changes to one with fine evenly distributed granules, and the whole contents assume a much lighter appearance. After 15–30 minutes one can discern the formation of areas surrounded by faint granular but irregular lines. These become rapidly more prominent, and in a few minutes a slight movement can be detected within the zoosporangium. The areas represent the zoospores and their discharge is about to take place (fig. 8). The papillae of dehiscence, sometimes numbering as many as eight, become more and more extended and refractive until one or more finally break open, permitting the zoospores to escape. They pass out in single file, at first rather rapidly, then more slowly as the pressure within the zoosporangium becomes lessened (fig. 56). Being of a plastic nature, they squeeze through the opening, arriving at the outside irregular in form, and very commonly with their cilium held in the opening by the next emerging zoospore. After a few seconds they move slowly away, assuming their normal form.

The zoospores are oval to elliptical, not infrequently slightly ovate, in which case the narrower end is the anterior one. The number of cilia varies from one to three, and they are attached at the posterior end. From a large number of careful examinations of both living and stained preparations of zoospores, I assume that the uniciliated condition is the typical one, as it occurs much more frequently than the other two types. The triciliated zoospore is rarely seen, while the biciliated form is common. The zoospores of *B. Pringsheimii* possess, according to THAXTER (9), one or two

cilia. He considered the latter number the typical one, while PETERSEN (4) has described the zoospores as uniciliate.

The zoospore contains a large subtriangular centrally located body which resembles a large nucleus (fig. 23). THAXTER observed this body and described it as follows: "The nucleus is very large and subtriangular in outline, its base connected with that of the cilia by a fine strand of protoplasm." Fig. 24 shows very distinctly the connection of the cilium with the base of the large central body. The zoospore was killed with a 1 per cent solution of osmic acid and stained with an alcoholic solution of Magdala red. In the process the outer portion of the zoospore broke away, leaving the cilium still attached to the central body as represented. There can be observed in properly killed and frequently in living zoospores a more or less hyaline globule situated at the base of the central body, which contains a highly refractive granule. This body is undoubtedly the nucleus of the zoospore and will be more fully discussed later. The zoospore also contains groups of large and small granules, evidently of a fatty nature, which are principally located in front and to the rear of the so-called central body.

In movement the zoospores proceed in a more or less direct course, with a slight swaying of the body, and at times accompanied by a slow rotation on the longitudinal axis. If supplied with sufficient oxygen they may continue to swim for a number of hours, but when mounted on a slide under a cover glass, where the oxygen supply is small, they soon cease movement and germinate.

Fig. 28 shows a section of a young reproductive body, presumably a young sporangium, stained with iron-alum hematoxylin. The protoplasm is granular, vacuolated, and contains distributed throughout it prominent nuclei and large and small deeply staining bodies to which reference has already been made. The number of nuclei is at first small, and there is apparently no marked passage of the nuclei from the adjacent portions of the mycelium such as occurs in the developing sporangia and sexual organs of many other Phycomycetes. The nuclei in the upper half of the sporangium are in various stages of division. This condition may be found in young rapidly growing hyphae and principally at the growing point. As growth proceeds the number of nuclei rapidly

increases, until 40–70 are produced, usually about 60 in average-sized sporangia. About the time the zoosporangium reaches its full size the nuclei arrange themselves about the periphery. A large number of the sections show this condition, which seems to indicate that the zoosporangia rest in this stage. This condition probably agrees with that described above for the living specimen in which the protoplasm is coarsely granular.

Fig. 29 represents a section of a zoosporangium which is entering the stage of zoospore formation. The large nuclei have become distributed throughout the more coarsely granular protoplasm. The number and size of the deeply staining bodies has increased, while some of them show a vacuolate condition. On some of the nuclei can be seen deeply staining masses of small size. Other nuclei are associating themselves, more or less closely, with some of the larger masses.

This condition is carried still farther in fig. 30. In a number of cases the nuclei are more or less imbedded in the deeply stained bodies, in others they are still free from them. These stages very probably correspond to the more or less homogeneous stage of the living zoosporangium which just precedes the differentiation of the zoospores. Fig. 30 also shows the beginning of segmentation of the protoplasm. It proceeds from the periphery inward in a more or less radial direction, much as described by HARPER (2) for *Synchytrium decipiens*. The lines of division are first recognized as rows of granules, at first more or less indefinite, but which become more and more apparent until they are seen entirely to outline the spore mass.

Fig. 31 represents a part of a section of a sporangium in which segmentation is almost complete. The limiting surfaces of the spore masses in a number of cases have separated. Apparently contraction has taken place, which would indicate that the mature zoospores occupy less space than the original masses of protoplasm from which they are formed. HARPER (2) observed that shrinkage of the protoplasm takes place in the early stages of cleavage in *Synchytrium decipiens*, and suggested a loss of water as the cause. He also observed the open spaces formed by the separation of the segmented masses.

It will be observed (fig. 31) that the nuclei with their associated material have assumed a more regular form. The nucleus itself is drawn out to a point which, in some cases, extends to the very limits of the spore. No indications of cilia have been observed at this stage, but they can be seen occasionally in a later stage, that is, at the time of discharge of the zoospores. The condition of the nucleus described strongly suggests that the cilia have their origin through its direct influence.

Segmentation usually results in the formation of uninucleate zoospores. Occasionally, however, one may find binucleate zoospores with the nuclei in the same or different central bodies, or what I shall hereafter call food masses or bodies. Fig. 34 shows normal zoospores ready to escape from the zoosporangium. Fig. 35 shows the two types of binucleate zoospores of the same age as those in fig. 34.

In preparation for germination the zoospore comes to rest, takes on a spherical form, and gradually absorbs its cilium, which in the process commonly becomes enlarged at the end (fig. 25). The large reserve food body disappears and a large number of variously sized granules take its place. In the course of 10–20 minutes the germ tube makes its appearance and grows rapidly, forming the basis for the subsequently developed rhizoid system (figs. 26, 27, 2, *a–c*). The body of the zoospore forms the basal cell of the plant.

Fig. 36 represents a zoospore stained with iron-alum hematoxylin, preparing to germinate. As described above, the reserve food mass has apparently broken up into a number of deeply staining granules. As the germ tube elongates, the nucleus increases in size (fig. 38) and finally divides to form two (fig. 39). Accompanying the rapid growth of the young plant the protoplasm becomes more and more vacuolated and finally granular (fig. 40). Stained preparations of germinating zoospores beyond the four-nucleate stage were not obtained.

Just what the nature of the so-called reserve food bodies is has not been determined. Fig. 41 shows a zoospore killed with iodine solution. The nucleus and some granules show distinctly, while the large food body in most cases is invisible. Fig. 42, killed with weak Flemming solution, reveals that body clearly, and also the

blackened condition of the granules, which indicates their fatty nature.

Papillae of dehiscence occur on the zoosporangia of many Phycomycetes. In most cases they have been described as small swollen areas in the sporangial wall, or tips of exit tubes which become gelatinized and allow the emission of the zoospores to take place. An interesting condition is found in *Rhipidium americanum*. The zoosporangium possesses a double wall; the outer forms a cap over the papillae, which, on the discharge of the zoospores, becomes lifted up by the protruding inner wall; the latter forms a cylinder or vesicle which incloses the discharging zoospores; it ruptures immediately, setting them free (THAXTER 10). A similar condition prevails for *Sapromyces*.

So far as I have been able to learn, the structure and behavior of the papillae of *B. strangulata* differ from anything yet described. In the living sporangium the papilla possesses what appears to be an outer highly refractive hyaline convex cap, with a less refractive area between it and the protoplasm of the sporangium. The external part becomes more and more convex as gelatinization proceeds (fig. 8). Just before the disappearance of the outer part it loses its high refractive power to some extent, and has the semblance of glycerine. Suddenly the thin ungelatinized portion of the wall breaks, and becomes forced out, leaving a ragged rim, many times, about the opening. The adjacent gelatinized part is immediately dissolved in the surrounding water, and to all appearances the exit pore is open. In a few seconds the zoospores begin to escape. Under what seem to be normal conditions, a vesicle is formed which incloses at least a part of the zoospores on their discharge. This vesicle soon breaks and the zoospores are set free (fig. 13). Frequently no such vesicle can be seen, and in such cases the zoospores escape as shown in fig. 14. The formation of such an inclosing membrane immediately suggested a double wall to the zoosporangium, and also that it was the inner of the two which either protruded as in *Rhipidium americanum*, or that by its gelatinization it was enabled to stretch out in the form of a thin sac.

On the examination of sections it was found that neither assump-

tion was correct. Fig. 9 shows a section through an immature papilla and the adjacent wall of the zoosporangium. It is very evident that the wall is single, but that there are two distinct parts to the gelatinized plug of the papilla. The plug has a strong affinity for stain, especially safranin. The ungelatinized part of the wall is seen as a thin unstained layer extending over the convex plug. The wall immediately surrounding the papilla is thickened so as to form a sort of collar. This is clearly seen in empty sporangia. Fig. 10 shows the two parts of the plug separated as a result of cutting the section. It will be seen that the inner portion bears a close relation to the protoplasm. Such a section is common. In those sections which show a contraction of the protoplasm from the wall of the zoosporangium, almost invariably it is found to adhere closely to the inner part of the plug, whether that remains in place or not. It is this part of the plug that has the less refractive power in the living state and that on stretching out forms the vesicle referred to above. Very probably gelatinization is brought about by the action of an enzyme secreted by the protoplasm in the region about the papilla, which may account for the close relation between the two just described. Apparently the outer part of the plug becomes more thoroughly gelatinized than the inner, while the outer thin unstained part of the wall over the papilla is little or not at all affected.

This condition may be explained, it seems, by assuming that the wall of the zoosporangium is made up of lamellae which differ slightly in composition and which are differently affected by the gelatinizing agent. This assumption is strengthened by the fact that in a few sections the condition illustrated in fig. 9 was observed, that is, the line separating the two portions of the gelatinized plug extended slightly into the sporangial wall.

Development of resting sporangia

The resting sporangia agree in general to similar bodies described by REINSCH (**6**) and THAXTER (**9**) for *B. Pringsheimii*, and by THAXTER (**9**) for *B. ramosa*. In *B. Pringsheimii* they are called resting spores by THAXTER, and are considered as doubtful oospores by REINSCH. They are indicative of the older condition of the

plant, and when mature are deciduous. According to THAXTER, the mature resting spore is surrounded by two walls, an outer, thin and smooth, and an inner, thick and apparently perforated or pitted. He did not study a section of the wall, hence was not able to determine the structure definitely. They possess several large oil globules, are oval to pyriform, and vary in form almost as much as the zoosporangia.

In *B. ramosa* the resting sporangia, or spores, are "bluntly rounded, gradually narrower toward a truncate base, and about 30×11 μ." In this species the resting spores are less variable in form than those of *B. Pringsheimii*, but vary somewhat in size. The walls are very little thicker than those of the sporangia. Resting spores of neither species were seen to discharge zoospores or to germinate.

The resting sporangia of *B. strangulata*, for such they are, as will be shown later, are very constant in form and vary only slightly in size. They are ovate in form, with the narrower basal end truncate (fig. 15). As previously noted, they occur at almost any age of the plant, depending on the conditions of growth, and remain attached at maturity. They have their origin, in general, in the same manner as the zoosporangia, and in the younger stages cannot be distinguished from them. The wall begins to thicken early, and this, together with the absence of papillae, indicates that resting sporangia are developing. When they are mature they possess three walls, an outer and an inner, thin, smooth, and hyaline, and a middle, thick, perforated, and orange colored. The peculiar perforated nature of the middle layer can easily be made out in sections of mature resting sporangia. The pores are conical in shape, with the broad end outward. The greatest diameter is 0.8 μ and the least 0.3 μ. Fig. 16 shows a surface view, while fig. 17 is a diagrammatic representation of a cross-section, showing the pores and the inner and outer walls. The pores are more or less regularly arranged in rows, as seen in fig. 15.

The mature resting sporangia contain a number of oil globules which are not strikingly noticeable as they are in many other resting bodies of a similar nature. In describing these bodies for *B. Pringsheimii*, PETERSEN (4) says: "Peculiar pointed or rounded

cylindrical resting spores with a flat base and remarkably porous walls, without much content, appear in place of the zoosporangia."

In the young stages the protoplasm has much the same appearance as that of the young sporangia. Fig. 32 represents a section of a developing resting sporangium in which the nuclei are arranged about the periphery. The central mass of granular protoplasm, containing several reserve food bodies, is surrounded by prominent vacuoles. In the mature sporangium the protoplasm forms a definite regularly arranged network in which the nuclei are distributed (fig. 33). There are present, also, deeply staining masses, more or less irregular in shape, which probably represent the fusion of several reserve food bodies.

On germination the contents of the resting sporangia escape in the form of zoospores not unlike those formed in the zoosporangia. According to all observations and tests made, it is necessary that the resting sporangia pass through a period of rest before germination. I have not found any to germinate that were not at least one month old. This applies to cultures developed both in water and on agar. On the transference of the sporangia to fresh water there is no apparent change for some time. After 18–20 hours the two outer walls become cracked open, due very probably to the absorption of water. Sometimes they crack in several places, bringing to view the inner hyaline wall which bears one or more papillae of dehiscence. In a short time the normal discharge of zoospores takes place (fig. 22).

Nuclear division

The resting nuclei are usually spherical in form and contain a large deeply staining body which I assume to be a chromatic nucleolus. Surrounding this body is a fine granular cytoplasm which can be seen forming an irregular network (fig. 43). They vary in size from very small, almost invisible dots, to those with a diameter of 6–7 μ. The smaller are found in the actively growing parts where nuclear division more commonly takes place. The mode of division is rather unusual and suggests a form of amitosis. The first indication of such a nuclear division is a change of the chromatin mass from the more or less normal spherical to an elongated form (figs. 48, 52). A transverse line of division is next

seen (fig. 47). The two parts then round up (figs. 45, 53), separate (figs. 49, 51), and appear as two large nucleoli. A wall is finally laid down between the daughter chromatin masses, and the two nuclei result (figs. 44, 55). Frequently nuclei may contain three of these bodies (fig. 50). Evidently one of the two daughter masses of the first division divided before any nuclear wall separated them.

In dividing nuclei stained with iron-alum hematoxylin, there is a faintly staining homogeneous substance connecting the separating chromatin masses, which suggests some sort of a spindle. Two explanations suggest themselves: (1) that we are dealing with direct nuclear division and that the faintly staining substance is the cytoplasm contracted about the dividing chromatin masses; and (2) that division is indirect and that the large chromatin mass represents a single chromosome.

It seems unusual, if not improbable, that such a highly differentiated plant in so many respects should possess only a direct method of nuclear division. The fact, however, that no sexual organs are known for any of the species of the genus may have some bearing on the question. HUMPHREY (**3**) found a very similar nuclear division to take place in the hyphae of *Achlya apiculata*. From all observations yet made, I am inclined to hold to the view that we are dealing with a peculiar type of mitotic division. Further studies concerning the question are contemplated.

Since the species appears to be a new one, I add here a description giving the more important characters as observed by the writer.

Blastocladia strangulata, nov. sp.—Main axis oval to cylindrical, divided at the base into a number of rhizoidal divisions; above giving rise to a one to several times dichotomously or umbellately branched system whose ultimate branchlets produce terminally or subterminally zoosporangia and resting sporangia; definite constrictions and perforated pseudo-septa at the points of branching. Zoosporangia, oval to nearly spherical (50–63×40–52 μ), possess several papillae of dehiscence, and produce a comparatively small number of rather large zoospores. Zoospores 12×8 μ, with one to three cilia, usually one. Resting sporangia ovate to nearly oval, with a truncate base, 45×35 μ; the wall consists of

three layers, the middle thick, perforated, and orange colored; on germination giving rise to zoospores. Whole plant 200–2000 μ high, its main axis 40–100 μ in diameter.

Found but once, and on an aphid in a water culture made from soil taken from the bottom of an almost dry inland pond near Ithaca, N.Y.[2]

Axi primario ovato ad cylindricum, basi divisionibus rhizomatoideis numerosis, sursum copiose dichotome v. subdichotome ramoso; ramosis intervallis constrictis; pseudo-septis perforatis intra ramulorum basim formatis; zoosporangiis ovalibus ad sphaeroidea, 50–63×40–52 μ, papillas dehiscentes paucas ferentibus; zoosporis ovalibus, 12×8 μ, cilio plerumque simplici ornatis; sporangiis perdurantibus, rotundatis, basim versus graditim angustioribus et truncatis, 45×35 μ, zoosporis foventibus.

Hab. Ad aphid in aqua, Ithaca, N.Y.

Summary

1. The plant resembles in general the other species of the genus. Its mycelium is definitely constricted, which fact, it seems, definitely places the genus in the family Leptomitaceae.

2. It possesses peculiar perforated pseudo-septa which are formed at the constrictions, and which in a way are comparable to the "cellulin rings" of other members of the Leptomitaceae.

3. Zoosporangia are provided with a number of papillae of dehiscence distributed over the surface, which are formed as the result of the gelatinization of small circular areas of the wall. The resulting plug is made up of two distinct parts, the inner of which forms a vesicle into which the zoospores escape at the time of their discharge.

4. The zoospores possess a large centrally located subtriangular mass of apparently some reserve food substance, probably proteid in nature, at whose base is located the nucleus. They are typically uniciliated, with the cilium in direct relation to the nucleus.

5. Resting sporangia possess a three-layered wall; the outer and inner layers thin and hyaline; and the middle thick, perforated, and orange colored. After a period of rest of several weeks, germination takes place by the formation of zoospores.

[2] During May and June 1911 this species appeared several times in water cultures made from two garden soils one-fourth mile apart near Urbana, Ill. As it was found in soil collections made at different times and parts of the gardens, it was evidently not rare in those particular locations.

6. On germination the zoospore produces a germ tube which forms the basis of the rhizoid system, while the body of the spore becomes the basal cell of the plant.

7. Nuclear division is somewhat unusual, apparently, and reminds one of amitosis. It seems to the writer, however, that it is more probably a form of mitotic division dealing with a single large chromosome.

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EXPLANATION OF PLATES XVIII–XX

FIG. 1.—Biciliated zoospore.

FIG. 2.—Different stages in the germination of the zoospore.

FIG. 3.—Young plant with basal cell showing rhizoids and two branches which are beginning to branch dichotomously.

FIG. 4.—Young plant started on potato agar and subsequently transferred to water where sporangial development took place.

FIG. 5.—Plant similar to the one shown in fig. 4, with an empty sporangium and another almost mature below it.

FIG. 6.—A branch with sympodial arrangement of resting sporangia.

FIG. 7.—Resting sporangia more closely arranged on the branchlet, a more frequent condition in old cultures.

FIG. 8.—A mature sporangium showing zoospores differentiated and two papillae of dehiscence.

FIG. 9.—A stained section of a papilla of dehiscence.

FIG. 10.—Another section of a papilla of dehiscence, showing the protoplasm and attached inner portion of the plug drawn away from the wall.

FIG. 11.—Early stages in the development of zoosporangia.

FIG. 12.—A mature plant, showing the rhizoid system, manner of branching, and arrangement of reproductive bodies.

FIG. 13.—A mature sporangium discharging its zoospores into a thin vesicle which soon ruptures.

FIG. 14.—A mature zoosporangium discharging its zoospores without the formation of a vesicle.

FIG. 15.—Resting sporangium, showing the relative position of the pores in the much thickened wall.

FIG. 16.—An enlarged portion of the surface of a resting sporangium.

FIG. 17.—A diagrammatic representation of a microscopic section of the wall of a resting sporangium.

FIG. 18.—Different stages in the development of the pseudo-septa located at definite constrictions in the hyphae.

FIGS. 19–21.—Microscopic sections through such a septum as shown in fig. 18, *a*, giving the various appearances that result.

FIG. 22.—Germinating resting sporangium: outer walls cracked open, exposing the inner thin wall bearing papillae of dehiscence.

FIG. 23.—A zoospore showing the nucleus with its accompanying mass of reserve food material, and two cilia.

FIG. 24.—Zoospore killed with a 1 per cent solution of osmic acid and stained with Magdala red; the outer portion of the zoospore broke away, leaving the reserve material and nucleus with the single cilium attached.

FIG. 25.—Zoospore coming to rest preparatory to germination; contraction of the cilium taking place and contents becoming granular.

FIGS. 26, 27.—Early stages in germination of the zoospore: from living specimens.

FIG. 28.—Section of a young zoosporangium, showing nuclei in division and also several large deeply staining food bodies.

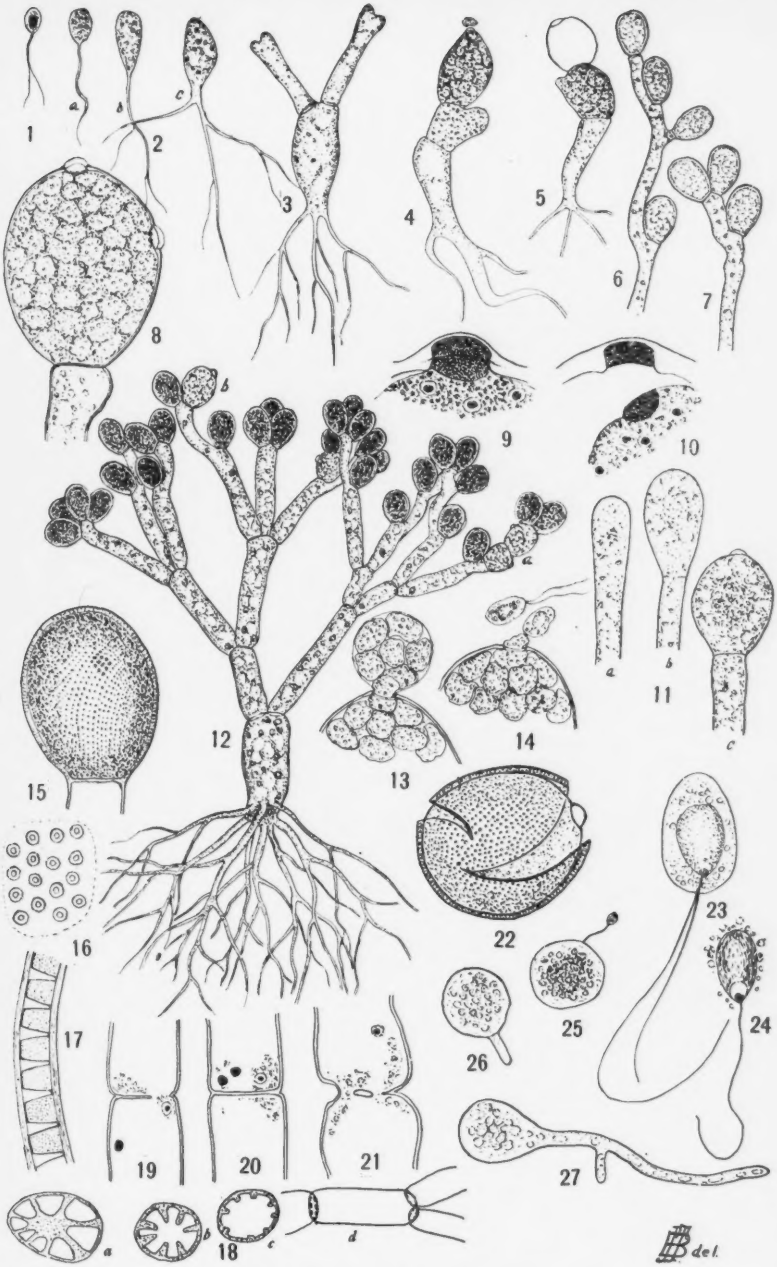
FIG. 29.—Section of a zoosporangium at the time of early nuclear association with the reserve food material preparatory to zoospore formation.

FIG. 30.—Later stage than that shown in fig. 29: many nuclei more or less imbedded in the reserve food material; lines of segmentation appearing at the periphery.

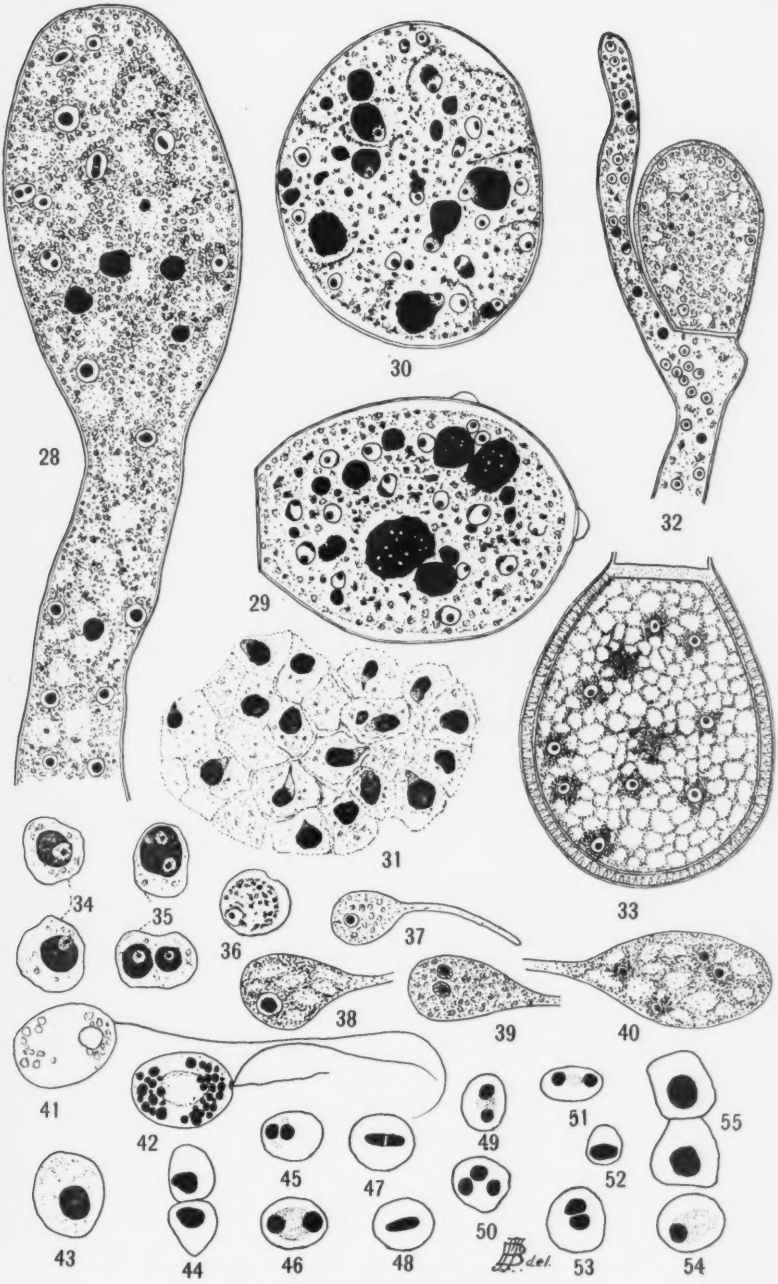
FIG. 31.—Section of a zoosporangium in which segmentation has taken place.

FIG. 32.—Section of a developing resting sporangium and a sub-branch.

FIG. 33.—Section of a mature resting sporangium.



BARRETT on BLASTOCLADIA



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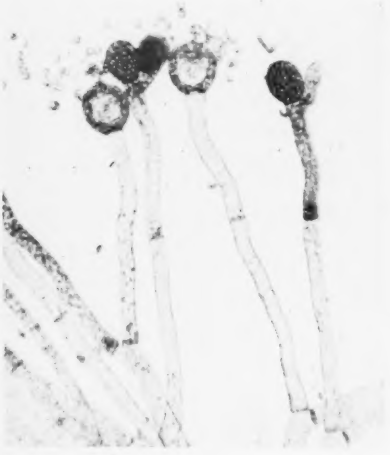

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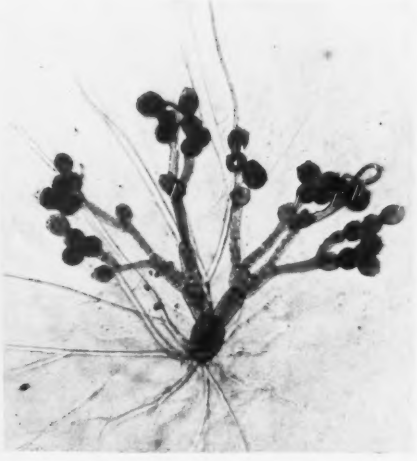

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BARRETT on BLASTOCLADIA

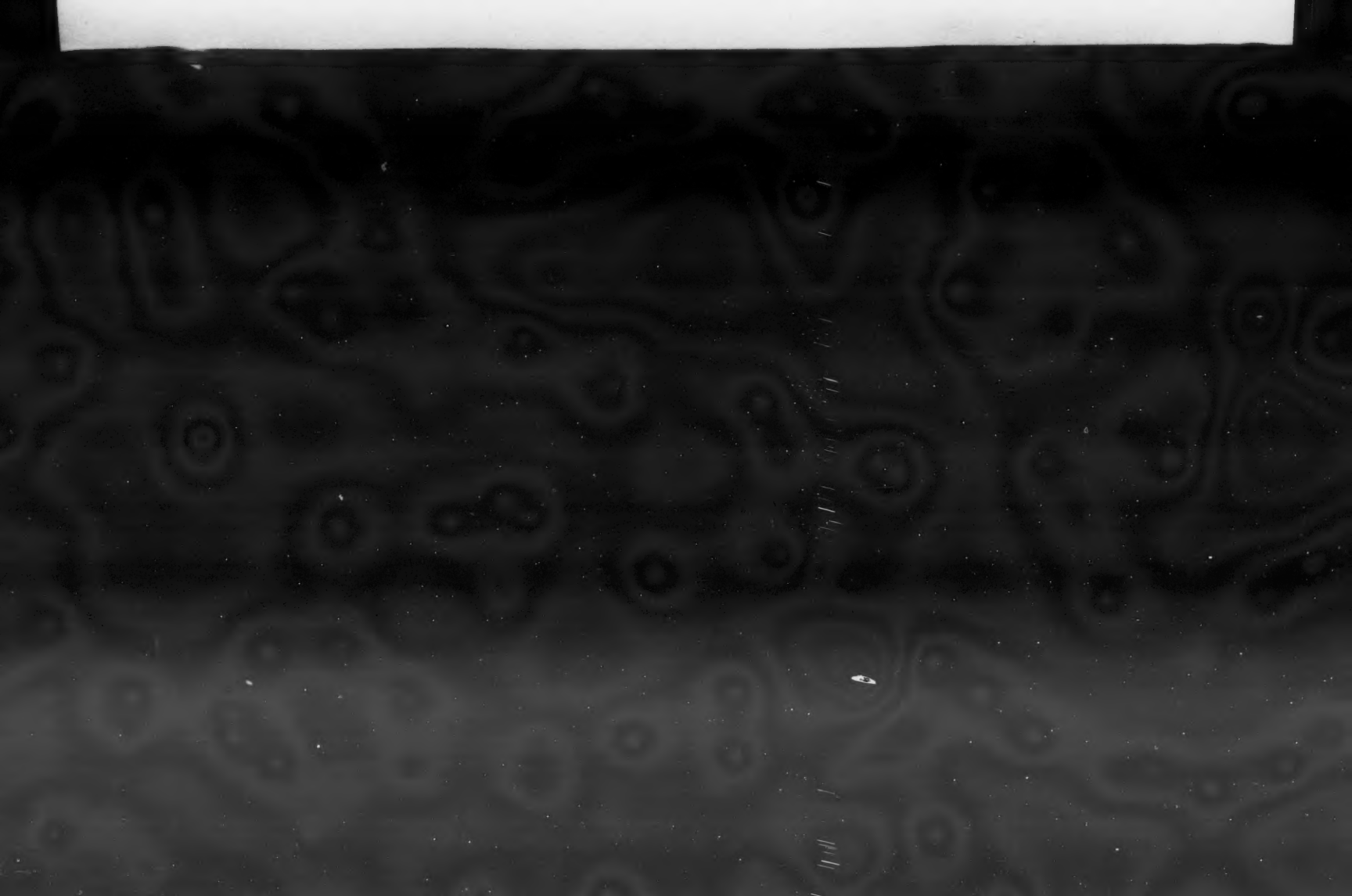

FIG. 34.—Stained zoospore from a ripe zoosporangium: nuclei very distinct; iron-alum hematoxylin.

FIG. 35.—Binucleate zoospores.

FIG. 36.—Zoospore preparing for germination: the large reserve food body is broken up into small granules.

FIG. 37.—Uninucleate germinating zoospores.

FIG. 38.—Germinating zoospore showing the large nucleus just previous to diyision.

FIG. 39.—Binucleate stage of a germinating zoospore.

FIG. 40.—More advanced condition of a germinating zoospore.

FIG. 41.—Zoospore killed with iodine: nucleus clearly shown, but the food body is invisible.

FIG. 42.—Zoospore killed with weak Flemming's solution: granules surrounding the nucleus and reserve food body stained black.

FIG. 43.—Resting nucleus, showing a large deeply staining chromatin mass surrounded by faintly staining cytoplasm.

FIG. 44.—Late stage in the division of a nucleus.

FIGS. 45–55.—Various stages of nuclear division.

FIG. 56.—A photomicrograph of zoosporangia discharging zoospores, and resting sporangia.

FIG. 57.—A photomicrograph of the plant from which fig. 56 was taken.

FIG. 58.—A photomicrograph of a small entire plant.

FIG. 59.—A photomicrograph of a young plant grown on agar, which shows the arrangement of zoosporangia in chains.

THE ORCHID EMBRYO SAC[1]

LESTER W. SHARP

(WITH PLATES XXI–XXIII)

During the spring of 1910 it was the writer's privilege to visit the island of Jamaica as one of a party of botanists from the Johns Hopkins University under the leadership of Professor D. S. JOHNSON. In view of the number of orchids available in the region visited, it was suggested by Professor JOHNSON that a study of the embryo sacs of these species, together with those of certain forms growing in the University's greenhouse at Baltimore, might for several reasons prove of value.

The orchids, standing at the end of a great evolutionary line, the monocotyledons, and reaching extreme specialization in other features, may be expected to show instructive deviations from the usual type of embryo sac, and it is through a study of such deviations that a final explanation of the origin and nature of the angiosperm embryo sac will probably be reached. They should also be most likely to reveal the end result in the reduction of the female gametophyte, which is seen occurring as one passes from the lower heterosporous groups to the higher. Furthermore, the data at hand on the orchid embryo sac, in part very suggestive, have been somewhat scattered, the details being well known in comparatively few forms, so that we have not known just what relation the cases reported bear to any general situation which may be present among orchids.

Although the number of additional species here described is small for a group as large as the Orchidaceae, they are well scattered throughout the family, so that taken together with species previously described they place us in a better position to draw conclusions on the general tendency of the group.

For the sake of clearness the different forms will be considered separately, and only two or three of them in detail.

[1] Botanical contribution from the Johns Hopkins University. No. 25.

Epidendrum variegatum Hook.

The course of development in this species corresponds in many respects very closely to that recently reported for *Epipactis pubescens* (BROWN and SHARP **2**), in which an 8-nucleate sac of the ordinary type is derived from one or less frequently from four megaspores. In *Epidendrum variegatum*, while the majority of sacs developed from one megaspore, the proportion of cases in which four are concerned is apparently greater than in *Epipactis*.

The archesporial cell, as in all of the other species examined, is hypodermal in position, and since it cuts off no parietals it is at the same time the megaspore mother cell. After passing through synapsis (fig. 1) and the other prophases preceding reduction, the nucleus of this cell divides. The position of the spindle and the wall formed upon its fibers is variable, which seems to be an important factor in determining the nature of the subsequent development. The spindle may be formed near the micropylar end of the mother cell, the resulting daughter cells in this case being very unequal in size, or the spindle may arise near the middle, the daughter cells then being approximately equal. Between these two positions of the spindle all gradations are found.

In the event of an unequal division the subsequent development is as follows. The small micropylar daughter cell at once begins to disorganize, while the large inner one divides (fig. 2) to form two megaspores. Of these the inner one only remains functional, the outer one disorganizing along with the micropylar daughter cell (fig. 3). The nucleus of the functioning megaspore divides without the formation of a wall (fig. 4) and the resulting nuclei again divide freely to form the 4-nucleate sac (fig. 5). At the next division (fig. 6) cell plates appear on the fibers of all four spindles, but those formed in connection with the chalazal nuclei usually disappear, so that the antipodals are in most cases represented by free nuclei.

When the division of the megaspore mother cell is equal (fig. 7), the cell plate which forms upon the spindle fibers is ephemeral and the two daughter nuclei are left free in the same cell cavity. Vacuolation occurs in the cytoplasm, usually in the region between the nuclei (fig. 8), but at times near the ends of the cell with the two nuclei at the center (fig. 9). At the division of these nuclei distinct

cell plates appear on the spindle fibers but do not persist, so that the four resulting nuclei remain free in the cytoplasm (figs. 10, 11). Since these have arisen by two successive divisions from the nucleus in which the heterotypic prophases occur, they are to be regarded as megaspore nuclei, and any one of them is thus the morphological equivalent of the nucleus shown in fig. 3. By one further division these four megaspore nuclei give rise to an 8-nucleate sac similar in all essential points to that derived from a single megaspore. An egg apparatus of the ordinary type is organized; the antipodal nuclei may or may not be separated by walls; and the two polar nuclei meet in the vicinity of the egg (fig. 12).

The various stages described in the foregoing paragraph may be distinguished from those in the development of a sac from a single megaspore by the absence of disorganized cells at the micropylar end. In later stages these latter become indistinguishable from the disorganized contents of the epidermal cells of the nucellus, so that it is then unsafe to use them as evidence, but there appears to be nothing against the assumption that the fate of the embryo sac is the same whether it has been derived from one megaspore or from four.

In this *Epidendrum*, as in *Epipactis*, two megaspores evidently take part in the formation of the embryo sac in a few cases. This condition results when the division of the megaspore mother cell is very unequal and that of the inner daughter cell equal, the separating wall at the second mitosis being ephemeral.

The pollen tube enters the sac, disorganizes the two synergids, and liberates two male nuclei. One of these fuses with the egg nucleus, while the other fuses with the two polars (fig. 13). The endosperm nucleus formed by the latter fusion undergoes no division, but degenerates along with the three antipodal nuclei (fig. 14).

The first few divisions of the fertilized egg are transverse, resulting in a filamentous proembryo of a varying number of cells. Longitudinal walls soon come in, and for a time the cells show a very regular two-ranked arrangement (fig. 15). Fig. 16 represents a proembryo of *E. verrucosum*, in which the number of transverse divisions has been very high, forming a filament of about 20 cells.

Figs. 17 and 18 show two stages in the development of the proembryo of *E. cochleatum*. In these three figures is seen the general course followed by the *Epidendrum* proembryo up to the stage found in the mature seed. Multiplication of cells commences at the chalazal end of the filament and extends upward, resulting in an oval mass of cells which is still to be regarded as a proembryo, since the body regions have not yet been marked out.

Epidendrum verrucosum Sw., **E. cochleatum** L., **and E. globosum** Jacq.

The embryo sacs of these forms were briefly examined. In the first two species stages were observed corresponding in all essential features to figs. 1, 3, 5, 12, and 14. In *E. globosum* were seen an ordinary 8-nucleate sac and a stage like that shown in fig. 14. It thus appears that *E. verrucosum*, *E. cochleatum*, and probably *E. globosum*, agree with *E. variegatum* in the formation of an embryo sac of the usual type from a single megaspore. The investigation of these three additional species was not carried far enough to determine whether they also show other methods of developing the embryo sac or not.

Phajus grandifolius Lour.

The early stages in the development of the embryo sac in this form correspond to those described above for those cases of *Epidendrum* in which but one megaspore is concerned in the formation of the sac.

The megaspore mother cell (fig. 19) divides unequally and the chalazal daughter cell again divides to form two megaspores. The outer daughter cell and megaspore disorganize (fig. 20), while the inner megaspore initiates the formation of the embryo sac. The nucleus of this functioning megaspore by two successive divisions gives rise to four; two of these lie at each end of the sac, the center of which is occupied by a large vacuole. The two chalazal nuclei undergo no further division, while those in the micropylar end divide to four (fig. 21), which become organized into an egg apparatus of the usual type and a free polar nucleus. This polar migrates toward the base of the sac and lies near the two chalazal

nuclei which have failed to divide (fig. 22). These three may fuse very soon (fig. 23) or they may remain distinct through the subsequent stages (fig. 24). In fig. 23 the egg apparatus fills an unusually large portion of the embryo sac.

The pollen tube discharges two male nuclei into the sac; one fuses with the egg nucleus and the other becomes associated with the free antipodal nuclei and micropylar polar (fig. 24). These latter nuclei show little regularity in behavior; they may begin to disorganize at any stage, but usually become more or less fused before this occurs. In any event no endosperm is formed.

The fertilized egg divides transversely to form a short filamentous proembryo, which attains a length of three or four cells before the first longitudinal division occurs. At this stage the cell toward the micropyle begins to elongate and push out into the surrounding placental tissue as a haustorial suspensor (figs. 25, 26). Later this dies away so that the proembryo in the mature seed is a simple rounded mass of cells (fig. 27).

Corallorhiza maculata Raf.

In *Corallorhiza* the embryo sac develops in a manner similar to that in *Phajus grandifolius*, as a comparison of figs. 28–33 (*Corallorhiza*) with figs. 20–24 (*Phajus*) will show. Consequently the above description of the sac of *Phajus* applies in all essential points to *Corallorhiza*, so that a separate account of the latter is unnecessary.

The proembryo of *Corallorhiza*, as described by LEAVITT (**6**), has a very long two-celled suspensor, which projects through the micropyle and enters the tissue of the placenta.

Broughtonia sanguinea R. Br.

This species shows the same peculiarity described above for *Phajus* and *Corallorhiza*. The innermost megaspore gives rise to a sac with six nuclei, the primary antipodal nucleus dividing only once. This division does not usually occur until the two nuclei in the micropylar end divide to four, so that three spindles are observed in the sac at one time.

Bletia Shepherdii Hook.

This form affords another example of the derivation of the female gametophyte either from one or from four megaspores, the course followed being apparently connected with the position of the wall formed at the division of the megaspore mother cell, as pointed out in *Epidendrum variegatum*. The nucleus of this cell goes into synapsis (fig. 34) and at its division the spindle may lie near the micropylar end of the cell or at its center. In the former case the daughter cells are very unequal in size; the small micropylar one degenerates, and the chalazal one divides to form two megaspores (fig. 35). Of these the outer one disorganizes, while the inner one enlarges and continues the development, by two successive divisions giving rise to the 4-nucleate embryo sac (figs. 36–38).

When the division of the megaspore mother cell nucleus occurs at the center of the cell (fig. 39) the wall formed is evanescent, the two nuclei thus being left free in the same cell cavity (fig. 40). These nuclei divide simultaneously, as shown in fig. 41; here the wall laid down at the first mitosis in the megaspore mother cell is still visible as a remnant, and several chromosomes are seen lying in the cytoplasm apart from the spindles. The four nuclei which thus arise, being the product of two successive divisions from the nucleus in which the heterotypic prophases occur, are to be regarded as megaspore nuclei (fig. 42).

Except for the absence of disorganized cells at the micropylar end, the 4-nucleate sac formed as just described is similar in appearance to that produced from a single megaspore (cf. figs. 38 and 42). Since the active growth of the sac results in the complete obliteration of the disorganized cells, it is not possible to determine by inspection of the later stages from which type of 4-nucleate sac they have been derived, but there seems to be no reason why either type or both should not continue the development, which from this point onward is exceedingly irregular. Abnormalities of many kinds were observed, and all that can be attempted here is to indicate one or two of the common tendencies shown.

In only three cases were there seen more than four nuclei in the embryo sac before fertilization. In one of these (fig. 43) the two micropylar nuclei had divided, resulting in a 6-nucleate sac like

that described above for *Phajus*, *Corallorhiza*, and *Broughtonia*. In each of the other two cases the antipodal nuclei had also divided, forming an 8-nucleate sac (fig. 44). In none of these sacs were walls observed separating the nuclei at either end.

Since no walls are present at the 4-nucleate stage, the nuclei are free to wander about through the sac (fig. 45). They were seen in all positions, but sooner or later they may all fuse to form one large nucleus. The most common course followed is that represented in figs. 46–48; the nuclei near each end of the sac fuse and the resulting fusion nuclei do the same. Often all four fuse at once; sometimes only two fuse; and in many cases degeneration sets in before any fusions have occurred.

Apparently the pollen tube may enter the sac and discharge its two male nuclei at any of these stages. In fig. 49 it has extended to an unusual distance into a sac like that shown in fig. 47, and in fig. 50 the male nuclei have been discharged into a sac containing three nuclei in the central region. As far as could be determined, no nucleus is set apart as the egg. The nuclei all lie in a group for a time, and when disorganization does not occur at once they may become fused (figs. 51–53). The large nucleus which results was not observed to carry the development any farther.

In the material sectioned embryos proved to be exceedingly scarce, and this condition is undoubtedly connected with the irregularity and lack of organization shown by the embryo sac. The two-celled proembryo in fig. 54 has evidently formed in a 6 or 8-nucleate sac, as beside the pollen tube there are in the micropylar end two disorganizing nuclei, probably synergids, and in the chalazal region a partially fused and degenerating group made up of at least three. The next few divisions in the proembryo are transverse (fig. 55), so that in its early stages it is filamentous, as in *Epidendrum*. Meanwhile the placental tissue develops rapidly from all sides, completely filling the cavity of the ovary, and the few proembryos found were lying in the small intervening crevices.

It is not unlikely that the great irregularity shown by *Bletia* as here reported may be due in part to the somewhat artificial conditions under which the plant grew in the greenhouse.

Coelogyne massangeana and Pogonia macrophylla

In each of these forms the embryo sac contains eight nuclei derived in the usual manner from a single megaspore.

As is well known, the ovules of orchids do not develop far unless pollination has occurred. In most of the species here reported the pollen tubes are found growing among the ovules before the prophases of the reduction division in the megaspore mother cell; in one or two species they are not present before the embryo sacs reach the 2 or 4-nucleate stage. In reciprocal crosses between *Phajus grandifolius* and *Bletia Shepherdii* it was found that in both cases the pollen tubes develop in great numbers and grow down into the ovarial cavity, in which ovules develop and produce embryo sacs in smaller numbers but in the same manner as after normal pollination. In no case, however, was fertilization or an embryo seen resulting from crosses between these two species. Thus the stimulus necessary to the development of ovules with embryo sacs may be furnished by foreign pollen incapable of effecting fertilization.

Discussion

The main point of interest brought out in the above descriptions is the variability in development within the species. It has been noted by several workers that while the embryo sac of one species of a genus or family is formed from the megaspore mother cell directly, the sac of another species of the same group may arise from one of a row of megaspores. The same variation within the species has occasionally been observed, as in *Salix glaucophylla* (CHAMBERLAIN **4**) and *Juglans cordiformis* (KARSTEN **5**). In the Orchidaceae the latter condition appears to hold in a number of cases, the fate of the megaspore mother cell apparently being determined very largely by the position of the spindles at the first two divisions, as pointed out above for *Epidendrum variegatum* and *Bletia Shepherdii*, and recently for *Epipactis pubescens* (BROWN and SHARP **2**).

This fluctuation results in a reduction in the number of divisions occurring between the megaspore and the egg. When a single

megaspore produces the 8-nucleate sac there are three such divisions; when a similar sac arises from a daughter cell, two megaspores thus taking part in the process, there are two divisions; and when the megaspore mother cell gives rise to the sac directly, four megaspores are involved and the egg is separated from the megaspore by but one division.

The tendency to mature the egg earlier and earlier in the ontogeny of the gametophyte is very conspicuous among gymnosperms, and it was hoped that among these very advanced angiosperms the end result of this specialization might be found—the megaspore itself functioning as an egg. The number of cases in which the elimination of but one more division would result in this situation is fairly large, and includes sacs with 4 nuclei (*Cypripedium*, PACE **7**), 8 nuclei (*Lilium*, various orchids, and many others), and 14 nuclei (*Pandanus*, CAMPBELL **3**). That the reduced condition is being approached by such a variety of ways allows us to expect with confidence to discover in some plant a situation exactly paralleling that in animals, in which the product of the reduction divisions at once becomes the egg.

Scarcely less striking than the variability within the species is the uniformity shown by the embryo sac throughout a group so varied in structure and habit as the orchids. In spite of the inconstancy in the methods of sac development the end result is remarkably uniform. The ordinary 8-nucleate sac, developed from a single megaspore, is the prevailing condition in the group. Beside the species here reported, it is found in *Calopogon* (PACE **8**), *Habenaria* (BROWN **1**), *Epipactis* (BROWN and SHARP **2**), *Gymnadenia* (WARD **10**), *Orchis* (STRASBURGER **9**), and others.

The influence of the surrounding conditions upon the behavior of the nuclei during the formation of the embryo sac has recently been considered in some detail (BROWN and SHARP **2**). The facts brought out in the present account lend further support to the idea there expressed, namely, that the causes for the behavior of the nuclei are to be sought largely in factors external to the nuclei themselves. The conditions under which the ovules of orchids develop within the ovary are undoubtedly much the same in the

various species, while the ovules themselves are almost exactly alike in structure, varying only in the matter of dimension. Thus since the archesporial cell in the different species has the same general form and initiates a series of stages developing under practically the same conditions, a general similarity in result is to be expected.

Whether a row of megaspores is produced or not seems, as already pointed out, to be largely dependent upon the position of the spindles at the first two divisions. But megaspore mother cell and functioning megaspore just before division are very much alike in size, shape, and surroundings, and are acted upon by similar external factors, so that whichever gives rise to the embryo sac the same course is followed and the same end is reached.

The 6-nucleate embryo sacs of *Phajus*, *Corallorhiza*, and *Broughtonia* seems to show a tendency toward a further reduction of the vegetative portion of the gametophyte.

In all of the species examined the endosperm nucleus, whether arising from the fusion of two or more nuclei, disorganizes without dividing, so that *Calopogon pulchellus* (PACE **8**), in which it may give rise to as many as four free nuclei, remains as the only known case where endosperm is developed in orchids.

Summary and conclusions

1. The archesporial cell in all of the species examined is hypodermal and cuts off no parietals, thus becoming at once the megaspore mother cell.

2. The megaspore mother cell in all of the forms studied divides to two daughter cells, the chalazal one of which divides to form two megaspores. The innermost megaspore gives rise to the embryo sac.

3. In *Epidendrum variegatum* and *Bletia Shepherdii* the megaspore mother cell often gives rise directly to the embryo sac; in such cases four megaspores take part in the formation of the sac.

4. In *Epidendrum variegatum*, *E. cochleatum*, *E. verrucosum*, *E. globosum*, *Coelogyne massangeana*, and *Pogonia macrophylla* the embryo sac is of the ordinary 8-nucleate type. In *Bletia Shep-*

herdii the development is very irregular, but in fully mature sacs eight nuclei are present.

5. In *Phajus grandifolius*, *Corallorhiza maculata*, and *Broughtonia sanguinea* the primary antipodal nucleus divides only once, so that the embryo sac contains but six nuclei: four micropylar and two chalazal.

6. Polar fusion occurs in all of the forms studied. In the 8-nucleate sacs the fusion is between two equivalent polar nuclei. In the 6-nucleate sacs the micropylar polar migrates to the chalazal end and there fuses with the two nuclei which have resulted from the division of the primary antipodal nucleus.

7. In all of the species in which fertilization was observed it is of the usual type; one of the two male nuclei fuses with the egg nucleus, while the other fuses with the two polars.

8. The proembryo commonly consists of three cells before the first longitudinal division occurs; in *Epidendrum* a filament of as many as 20 cells may be formed. In the mature seed the body regions have not yet been marked out in the proembryo.

9. In all of the species examined the endosperm nucleus disorganizes without dividing.

10. The ordinary 8-nucleate embryo sac produced by a single megaspore is the prevailing condition among orchids. The causes for the comparative uniformity throughout the group are to be sought largely in the conditions surrounding the developing nuclei.

11. The orchids show very commonly a marked variation within the species. This variability, seen chiefly in connection with megaspore formation, is resulting in making an embryo sac in which the egg is removed from the megaspore by a single division a conspicuous feature in the group.

12. Although endosperm has been eliminated and the seed reduced to a very simple structure, the orchids as a group show in their female gametophytes very little advance over other plants, especially those lower in the line of the monocotyledons.

13. Reciprocal crosses between *Phajus grandifolius* and *Bletia Shepherdii* show that in these species the stimulus necessary to the development of ovules with embryo sacs may be furnished by foreign pollen incapable of effecting fertilization.

To Professor DUNCAN S. JOHNSON are due acknowledgments for many valuable suggestions during the progress of the work. The writer is also indebted to Mr. WILLIAM HARRIS for placing at his disposal material in the Hope and Castleton Botanic Gardens.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES XXI–XXIII

All figures were drawn with the aid of an Abbé camera lucida, and show magnifications as follows: figs. 1–15, ×1200; figs. 16–18, ×295; figs. 19–24, ×1125; figs. 25, 26, ×513; fig. 27, ×295; figs. 28–33, ×1200; figs. 34–54, ×845; fig. 55, ×475.

PLATE XXI

Epidendrum variegatum Hook.

FIG. 1.—Synapsis in megaspore mother cell.

FIG. 2.—Inner daughter cell dividing; outer daughter cell disorganizing.

FIG. 3.—Functioning megaspore: outer daughter cell and megaspore disorganized.

FIG. 4.—Two-nucleate embryo sac: no wall on lingering spindle fibers.

FIG. 5.—Four-nucleate embryo sac.

FIG. 6.—Division to form eight nuclei.

FIG. 7.—Megaspore mother cell dividing equally; distinct wall formed.

FIG. 8.—Wall has disappeared; vacuole has formed.

FIG. 9.—Unusual arrangement of nuclei and vacuoles; nuclei in this case have gone into resting condition.

FIG. 10.—Division to form four nuclei; distinct cell plates formed.

FIG. 11.—Four-nucleate embryo sac (four megaspore nuclei): walls have disappeared.

FIG. 12.—Eight-nucleate embryo sac.

FIG. 13.—Double fertilization.

Fig. 14.—Young proembryo: endosperm nucleus and antipodals disorganized.

FIG. 15.—Proembryo.

Epidendrum verrucosum Sw.

FIG. 16.—Filamentous proembryo.

Epidendrum cochleatum L.

FIGS. 17, 18.—Two stages of the proembryo.

PLATE XXII

Phajus grandifolius Lour.

FIG. 19.—Synapsis in megaspore mother cell.

FIG. 20.—Functioning megaspore: other daughter cell and megaspore disorganized.

FIG. 21.—Micropylar nuclei dividing; chalazal nuclei remaining undivided.

FIG. 22.—Six-nucleate embryo sac.

FIG. 23.—Same: egg apparatus formed; chalazal nuclei and micropylar polar fusing.

FIG. 24.—Fertilization: second male nucleus associating with other free nuclei of the sac.

FIGS. 25, 26.—Proembryo showing micropylar cell growing out as a haustorium.

FIG. 27.—Proembryo from mature seed.

Corallorhiza maculata Raf.

FIG. 28.—Inner daughter cell of megaspore mother cell dividing; outer daughter cell disorganizing.

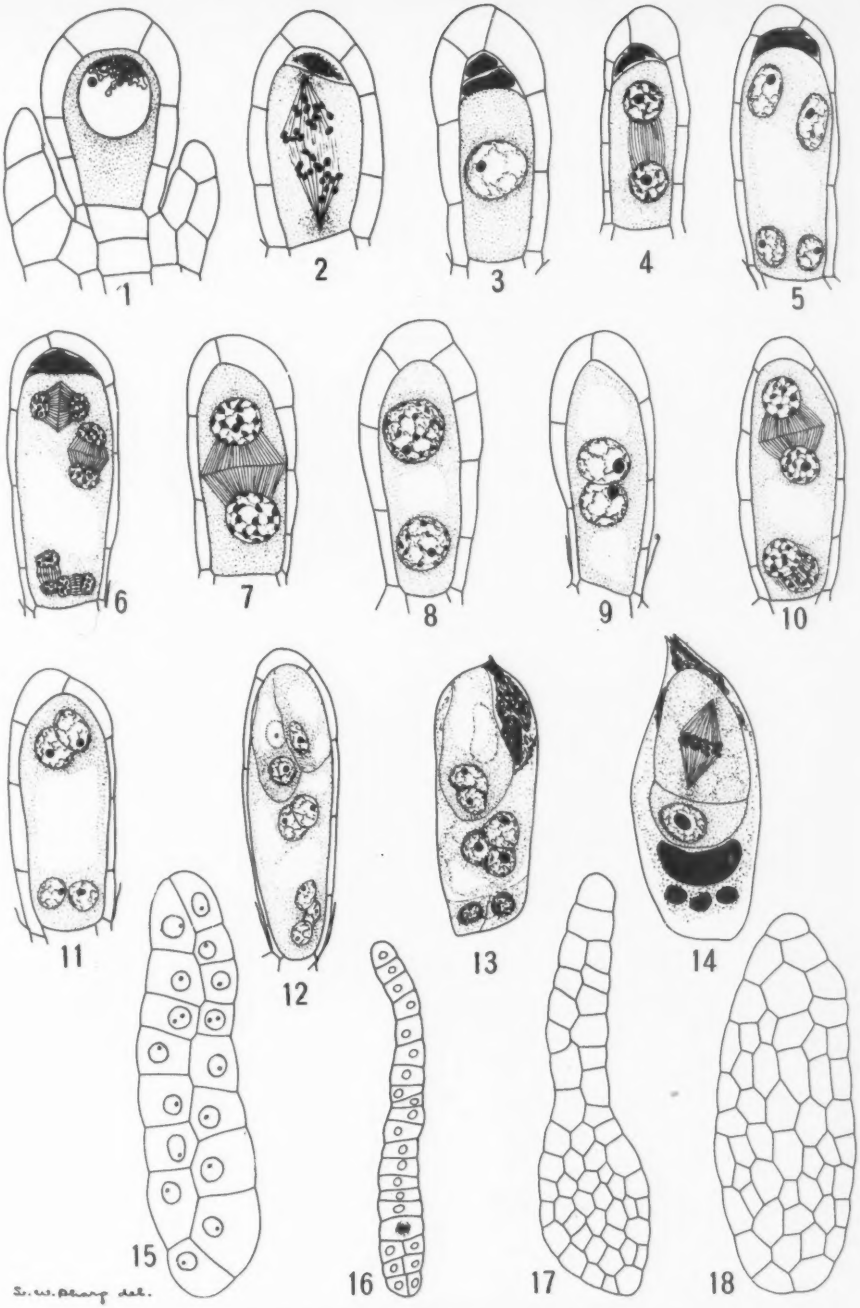
FIG. 29.—Four-nucleate embryo sac.

FIG. 30.—Micropylar nuclei dividing.

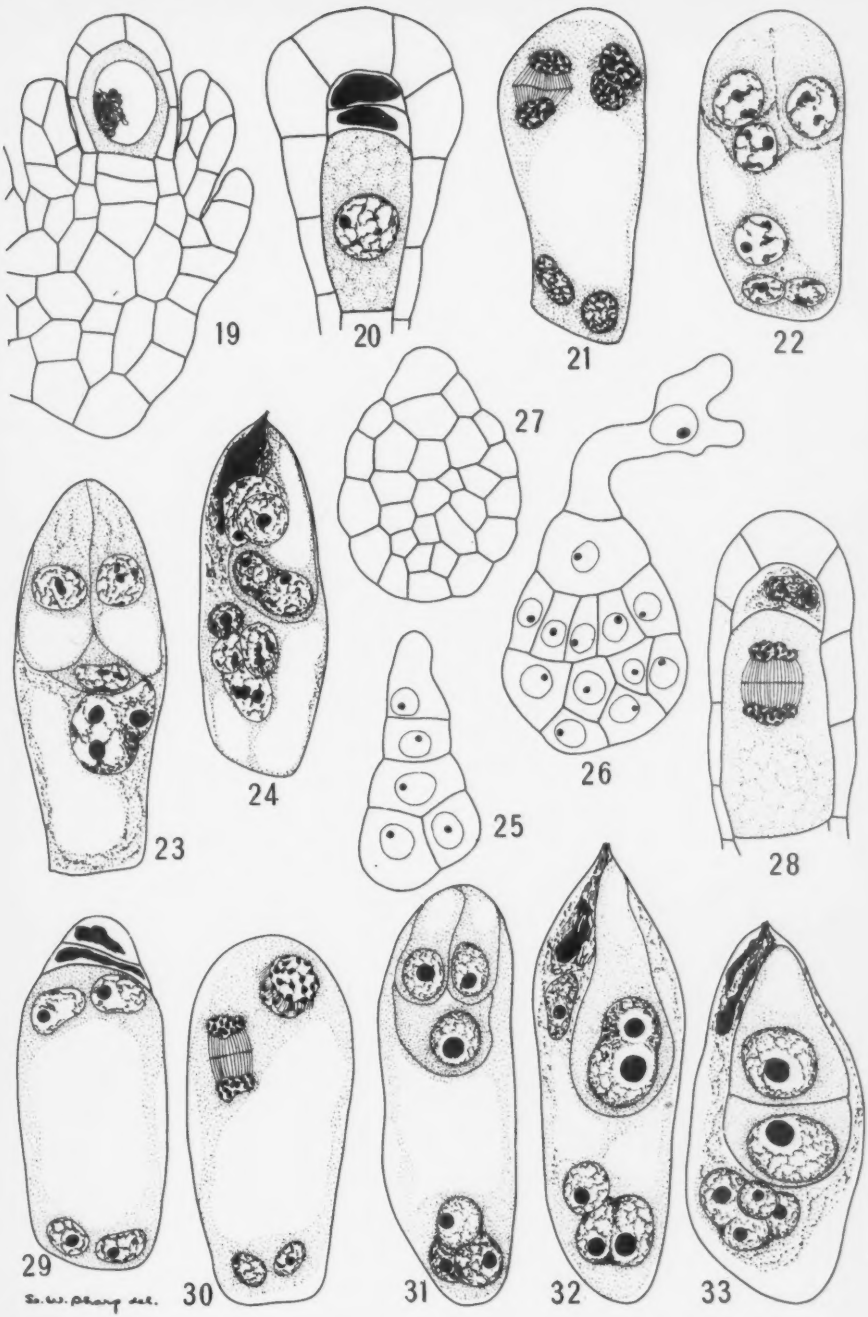
FIG. 31.—Six-nucleate embryo sac: micropylar polar has migrated to base of sac.

FIG. 32.—Fertilization has occurred; second male nucleus lying near egg.

FIG. 33.—Young proembryo: second male and other free nuclei of the sac fusing.



SHARP on ORCHID EMBRYO SAC



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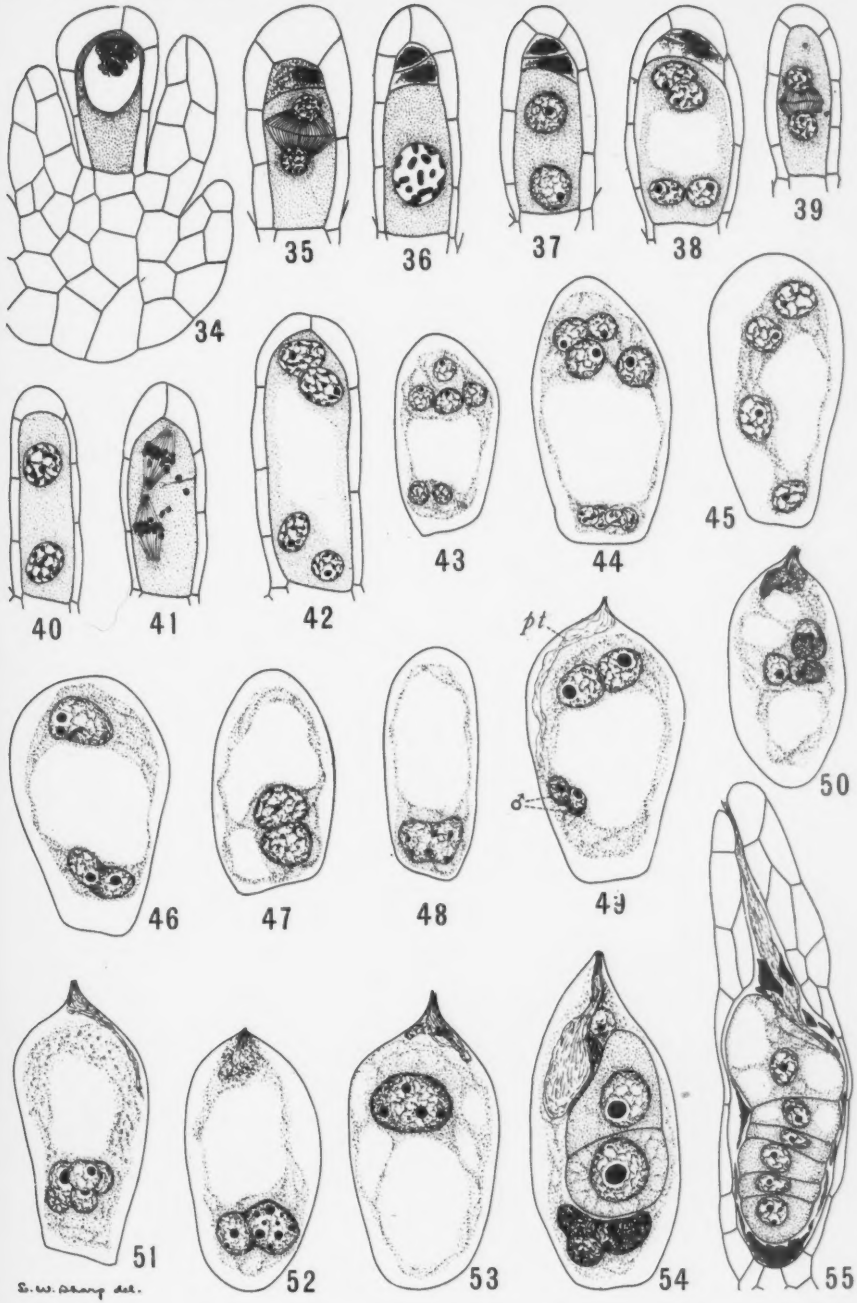

SHARP on ORCHID EMBRYO SAC

PLATE XXIII

Bletia Shepherdii Hook.

FIG. 34.—Synapsis in megaspore mother cell.

FIG. 35.—Inner daughter cell dividing to form two megaspores.

FIG. 36.—Functioning megaspore: outer daughter cell and megaspore disorganized.

FIG. 37.—Two-nucleate embryo sac.

FIG. 38.—Four-nucleate embryo sac.

FIG. 39.—Megaspore mother cell dividing equally; wall forming.

FIG. 40.—Wall has disappeared.

FIG. 41.—Two nuclei dividing: wall formed at first mitosis still visible as a remnant in this case.

FIG. 42.—Four-nucleate embryo sac (four megaspore nuclei).

FIG. 43.—Six-nucleate embryo sac: micropylar nuclei have divided.

FIG. 44.—Eight-nucleate embryo sac: no separating walls.

FIG. 45–48.—Usual fate of the 4-nucleate embryo sac; all the nuclei fuse.

FIGS. 49–53.—Abnormal sacs into which male nuclei have been discharged; all the nuclei tend to fuse; *pt*, pollen tube; ♂, male nuclei.

FIG. 54.—Young proembryo evidently having formed in a normal sac.

FIG. 55.—Later stage of proembryo.

GROWTH STUDIES IN FOREST TREES

I. PINUS RIGIDA MILL[1]

HARRY P. BROWN

(WITH PLATES XXIV AND XXV)

The phenomenon of tree growth has long been a subject of investigation. SACHS, HUGO DE VRIES, NÖRDLINGER, MER, the HARTIGS, WIELER, BÜSGEN, VON MOHL, and a host of others have worked on problems concerned with it, and many papers presenting the results of investigations are to be found in the literature of the last half-century.

As might be expected, the question has resolved itself into a number of minor topics, each with its coterie of followers. Some have placed particular stress on spring and summer wood formation; others have studied growth as related to external factors or to inheritance. Various instruments have been devised to measure tree growth, and one author (REUSS **12**) goes so far as to assert that thunderstorms cause a growth stimulus in trees. Investigations dealing with every phase of the subject are described in exhaustive detail, and yet with rare exception there is a maze of conflicting opinion sufficient to confuse even the careful reader.

The present studies were undertaken with a twofold purpose, namely, to clear up disputed points regarding annual ring formation in trees and to formulate laws of tree growth. Investigations were carried on upon various forest trees with this idea in view. The results of those on *Pinus rigida* are embodied in this paper.

Secondary thickening in trees arises as a general rule from a cambium which lives from year to year. This annually passes through certain active and certain dormant periods. The latter assertion, however, is to be taken in its broadest sense. In many tropical woods the interruption to growth can be detected only with a microscope, while in others it is totally lacking; the wood appears

[1] Contribution from the Department of Botany, Cornell University. No. 148.

as a homogeneous mass. The formation of this cambial layer takes place the first year, and is brought about by the linking together, so to speak, of the fascicular cambium of the primary bundles by the formation of interfascicular cambial zones, the result being a cylinder of merismatic tissue capable of division. There are, in addition to this, however, certain other growth phenomena. In the cortéx of many trees, either near or remotely distant from the primary cambium, secondary cambial zones arise, whose function it is to form cork, the so-called cork cambiums. They are not united in a ring, as is the primary cambium, but extend for comparatively short distances in a peripheral direction.[2] Again, as met with in the Cycadales and Gnetales (COULTER and CHAMBERLAIN 4), successive bundle-forming cambiums sometimes arise toward the periphery of the stem, and in such cases the life of the primary cambium is generally very short. Further, among dicotyledons there are a number of modifications of secondary thickening, particularly in underground parts. In the present studies, however, it is the intention to confine investigation to growth as it normally occurs in trees, that is, to the activities of a cambium which has certain active and certain dormant periods.

A number of specimens of *Pinus rigida* in the Cornell pinery as well as others in the wild state were used. Those in the nursery consisted of a number of individuals standing in a row which ran approximately east and west. The land sloped gently to the southwest and drainage conditions appeared to be good. The individual trees were about 22 years of age and seemed to be in a thriving condition. The height varied from 6 to 7 m., depending on the vigor of the individual, and the average diameter at breast height was 12 cm. In 1909, when investigation began, the branches extended to within 1.2 m. of the ground. However, during the year above mentioned, the trees were pruned to a height of 1.9 m. above the ground. Experiments were carried on with six individuals of this series, which were numbered I–VI.

The trees in the wild state had better be described separately, since each was of different age and external factors varied with the individual. For the sake of clearness they were designated as

[2] Exceptions to this rule occur, resulting in the so-called "ring-barked" trees.

A, *B*, and *C*. These specimens were growing in a strip of woodland about one mile north of the university campus. Conditions of soil and light appeared to be good in every case, that is, to all appearances the trees were not retarded.

Tree *A* was a magnificent specimen about 25 m. high; in other words, it had practically reached its maximum size. The trunk was slightly shaded to a height of 4.5 m. by an undergrowth composed of white pine. There were no branches above for 18 m. until the crown began. The latter was but fairly developed, being about what one might expect under forest conditions. At breast height, the caliper measure was 50 cm. A conservative estimate of the age would be 100 years.

Tree *B* was a younger individual. Its height was approximately 20 m., and crown development had progressed but poorly. At breast height the caliper measure was 26 cm. The base was entirely free of undergrowth, and light conditions were better inasmuch as there were no close neighbors. Tree *B* then differed from tree *A* in (*a*) age, (*b*) light conditions, (*c*) crown development, (*d*) height, and (*e*) diameter.

Tree *C* was about the age of those in the nursery, namely 20–25 years, and rose to a height of 7 m. Branches were borne practically to the ground. The caliper measure was 11 cm. Illumination was better on the south side, due to the close proximity of a road, while on the north the underbrush encroached slightly.

Methods

Investigations began in the spring of 1909, and the last cutting that year was made on July 6. Alternate cuttings were taken from two different individuals at intervals about a week apart, so that two weeks elapsed between incisions on any one tree. These were made in the following manner. Beginning from the base of the apical shoot, portions of the cortex and wood to a depth of at least one annual ring were removed at intervals of about 50 cm. Twelve cuttings were made in this manner with the aid of a sharp pocketknife, care being taken not to rupture the cambium. Each cutting was placed in a separate vial, properly labeled with the date, num-

ber of cutting, and tree, and kept separate from the others in all the successive processes of fixing and imbedding.

The following year (1910) cuttings were again resumed on the same trees, as well as on four more in the same row. The manner of procedure was identical with that above described except (*a*) every other cutting was omitted and (*b*) this season the first cutting was made February 21, the second April 2, and thereafter until the third of May. The object was to check up the results of the previous season and to make new observations. Two cuttings were also made on trees *A*, *B*, and *C* on April 27, one on the north side and one on the south. For purposes of comparison, one root cutting was taken from tree III on the same date.

Microscopical characters of the wood

As is characteristic of the Coniferae, the secondary wood of *Pinus rigida* is entirely devoid of vessels. It consists almost entirely of tracheids with bordered pits on their radial walls. In cross-section these appear regularly arranged in radial rows, which occasionally divide as they proceed toward the cambium. In longitudinal section they present the normal tracheid form, that is, a rectangular prism with sloping ends. The annual rings are sharply differentiated. Proceeding from the pith outward in radial direction are numerous pith rays; secondary rays arise in response to necessity; both are of the usual coniferous type. The histological characters of coniferous wood, however, have been described in detail by PENHALLOW (11), and the reader is referred to his excellent work for further detail.

The structure of the secondary thickening in the roots is quite closely related to that of the stem. However, there are one or two differences. The demarcation between the different rings is not so sharp. This results because the wood of the root is less dense than that of the stem. The tracheids possess wider lumina and there is less summer wood produced. In radial section the bordered pits on the walls are often biseriate, a condition which is never met with in the wood of the aerial portion.

Microscopical characters of cambium and cortex in winter condition

CROSS-SECTION

The radial rows of tracheids in the xylem continue directly out into the cortex (fig. 9) through the cambial zone. For a time this radial arrangement is maintained, but sooner or later it becomes irregular, due to certain changes which take place. The cambial zone in cross-section appears as a number of layers of cells with comparatively thin walls. It is impossible to pick out the initial layer. Exterior to this are the sieve tubes. These have wider lumina than the cells of the cambial zone, and the walls are thickened as much as or more than those in the summer wood section of the xylem. However, they are not lignified as are the latter. Companion cells are wholly lacking. The rows of bast parenchyma are very prominent. One row with a few scattered individuals is formed each year (STRASBURGER **13**), so that the thickened layers of sieve tubes are separated by thin bands of bast parenchyma. In the outer cortex the bast parenchyma cells become gorged with starch and greatly enlarged. As a result the older sieve areas are stretched tangentially and are seen as thin bands separating the larger cells. Pith rays appear as straight lines running out into the cortex, but as they proceed radially into the cortex they soon become more or less irregular and curved. There are no crystallogenous cells such as are described by STRASBURGER in *Pinus silvestris*. Exterior to the cortex proper there is a series of corky layers which have arisen from living cells in the outer cortex, the so-called cork cambiums. Their structure is of the general type described by STRASBURGER (**13**).

RADIAL SECTION

In radial section the cambial cells appear as prisms with sloping ends. The size varies slightly with the age. The sieve tubes have the general shape of the cambium cells from which they originate. Their radial walls are equipped with sieve plates, and these have the same location as the bordered pits on the walls of the tracheids. In radial section likewise we see to best advantage the bast parenchyma. This consists of rows of barrel-shaped cells arranged one

above the other. There is also a change in the pith rays. The ray tracheids have given rise to ray cells, so that the pith rays consist exclusively of the latter. These as well as the bast parenchyma cells contain abundant starch.

TANGENTIAL SECTION

In order to study cambium and cortex in tangential section, a series of mounts is necessary. The same general characters are observable, but in addition it is evident that there is an entire absence of sieve plates on the tangential walls of the sieve tubes. The callus thickenings of those on the radial walls, however, are particularly noticeable with proper staining (methyl blue).

Cambial awakening

In taking up the study of xylem formation as it normally occurs in trees, one naturally begins the study before cambial activity begins. Cuttings taken at different heights from tree III on February 21, 1910, all showed in cross-section the general outline of the completed ring. Growth was not manifest in any of the sections. Each ring presented well marked areas of early and late wood. The latter in *Pinus rigida* is sharply differentiated, owing to its greatly thickened walls. The above statement does not hold true, however, for the wood of the first two or three years at any point in the trunk. Here there is no sharp demarcation between early and late wood. This condition is probably brought about by the fact that the main axis was elongating rapidly at this point when the ring was formed, or else, as these investigations tend to show, growth is slow in beginning in the apical shoot but progresses very fast when once started, so rapidly in fact that there is not sufficient time for the walls to thicken appreciably. In either alternative, there is a gradual thickening in the walls of the late wood of successive rings as the apical shoot progresses aloft.

The next set of cuttings were taken on April 4, 1910, from tree III. The cambium was still in the resting condition. Figs. 1–3 and 7–9 show the changes which occurred (figs. 1–3) between April 4 and April 15. In fig. 3 growth is more advanced than in either figs. 1 or 2. The latter are both in the resting condition. So far

as can be detected there is no evidence of tracheal formation. Figs. 7–9 are from cuttings made on the same individual at this time, but each successively nearer the ground. In the first two growth is in evidence, while in the last the cambium is still in the resting condition. It is evident from the photographs that in the spring of 1910 growth made itself manifest in tree III as early as April 15. Cuttings taken from trees IV and V at the same date likewise showed evidence of cambial activity. While there was no satisfactory evidence obtained the previous year as regards cambial awakening, since observations were begun too late, sections from tree II on May 13, 1910, showed growth in such an advanced state that cambial activity must have begun fully as early the previous year.

As regards cambial awakening in trees *A*, *B*, and *C*, no lengthy observations were carried on; but two cuttings per tree were made on April 27, one on the north side and one on the south. At this date trees *B* and *C* already showed evidences of growth at breast height in both cuttings. In tree *A* the cambium was still in the resting condition. However, tree *A* was older and taller than the other individuals, and it is very evident that growth must have already begun in the higher parts.

The observations described above are in accord with those of other investigators. BÜSGEN (**3**) gives the time in general for cambial awakening for middle Germany as between the last half of April and the first half of May. R. HARTIG (**7**) has observed that evidences of growth are manifest in young (10 years) specimens of *Pinus silvestris* as early as April 20, while its appearance at the base of the older trees depended very much on external factors, such as thickness of stand, soil conditions, ground cover, etc. BUCKHOUT (**2**), by means of bark measure, gives the date of growth inception in larch and white pine as the last week in April. However, as his computations were made at the base of the trees, probably growth began aloft earlier. That growth was not evidenced at the base of tree *A* was due, according to the researches of R. HARTIG (**7**), to at least three causes, namely (*a*) long trunk, (*b*) age, and (*c*) shaded base. While the present investigations do not afford conclusive evidence, inasmuch as they covered but a

period of two years, it would appear that in the vicinity of Ithaca growth began in *Pinus rigida* at about the same time each spring. To determine this point definitely, however, observations must needs be carried on for a period of years. That growth made itself evident in 1910, however, as early as April 15 is readily apparent from the photographs.

Place of cambial awakening

The question of origin of growth is still in dispute. T. HARTIG (**8**) claimed that it made itself manifest in the youngest branches first and extended slowly downward. NÖRDLINGER (*Forest Botany*, 1874) makes the same assertion. R. HARTIG (**7**) appears to accept his father's statement if we are to judge from the following quotation: "Am oberirdischen Stamme beginnt der Zuwachs zuerst in den jüngsten Trieben," etc. These three investigators, therefore, were unanimous in the opinion that the awakening of growth is earlier at the top of a tree than below.

MER (**10**) disputes this general assertion. According to his researches, the procedure of awakening was sensibly different in older trees. While in 25-year-old oaks, beeches, and firs, growth was first manifest in the youngest branches, in the older trees it was in evidence at the same time at the bases of the branches and even in the trunk where the roots began. From these points growth gradually extended to the intermediate regions.

Figs. 4–6 correspond respectively to those of the preceding numbers, except that a period of 19 days intervened. Comparing those of different date, we see that growth is more in evidence in every case where the cutting was taken at the later date. In figs. 1 and 2 we have apparently the resting condition, while figs. 4 and 5 exhibit signs of growth, the latter being more in evidence in fig. 5. Comparing figs. 3 and 6, it follows that there is a considerable advance in growth. In the former, at the outside, only two half-formed tracheids are to be seen, while in the latter three or four rows are present and these are of larger size. Comparing figs. 1–6 as a whole, it is evident that during a period of 19 days there was an awakening of cambial activity in the apical portion, first manifest in fig. 3 on April 15. Growth first appeared in the crown of tree III

some distance below the apical shoot, but in a period covering 19 days gradually spread upward and was in progress in the apical shoot on May 4, 1910.

Cuttings of May 4 corresponding to figs. 7–9 were not photographed. Examination revealed the fact, however, that growth was in progress throughout the basal portion of the trunk on that date, and had progressed to a greater extent than was evidenced on April 15.

From the above investigations it follows that growth was in progress throughout the main axis of the tree on May 4, while 19 days previous it was not in evidence in either the apical portion or the base. If R. HARTIG is right in his assertion that growth is first manifest in the branches, *Pinus rigida* is surely an exception to the rule. MER'S investigations on *young* trees are in accord with HARTIG'S, so here likewise growth in *Pinus rigida* appears to present an anomaly. That HARTIG is right in his assertion that cambial activity proceeds from the base of the crown downward, investigations on trees *A*, *B*, and *C* seem to give convincing evidence. Cambial activity was already in progress on both sides of the base in trees *B* and *C* on April 27, while both cuttings in tree *A* on that date appeared to be in the resting condition. This is explained in that the trunk of tree *B* was better illuminated below than that of tree *A*, while tree *C* was but 25 years old. But at this date growth must have been in evidence in the upper portions of tree *A*, and the only reasonable hypothesis is that it had not yet reached the base, owing to poor insolation, thick bark, and age of the tree.

Growth in lateral branches

With a view of adding something further of value to the manner of growth procedure in *Pinus rigida*, investigations were also carried on upon certain of the lateral branches. Cuttings were taken from each year's growth until the main axis was reached. Then incisions were made 20 cm. above and a like distance below the point where the branch joined the main axis. Growth in the branches followed the same rule as in the main axis. It commences some distance back of the apical shoot and spreads gradually in both directions. Time of awakening in the apical shoots of the

branches, at least in the case of trees standing in the open, appears to be identical with that in the apical shoot of the main axis. Cuttings taken May 4 showed about the same amount of growth in each case.

The time of the beginning of cambial activity at the base of the branches is of interest when compared with that of the main trunk. Fig. 11 shows a section from the base of a limb six years old. Fig. 10 is from a cutting taken from the main axis just above the branch, and fig. 12 a like distance below. Growth is most advanced in fig. 12, present in fig. 10, but lacking to all appearances in fig. 11. Cuttings taken from the limb in question showed growth in evidence to the extent of one or two tracheids (out to and including the apical shoot). It follows from the above that growth at the base of the branches is more retarded than at neighboring spots in the main axis. It proceeds more rapidly in the latter than it does in the former, so that it is often in evidence in the main axis before it makes its appearance at the base of the branches. This may be due to the more rapid rise of solutions in the trunk, although further investigation is necessary to decide that point.

Rate of procedure

Having determined the general procedure of growth in *Pinus rigida*, observations were next made on the rate of procedure. In order to make estimates of this, the series of cuttings of 1909 on tree II were employed. There were four sets of these of twelve each. In each set the amount of wood formed for the individual section was determined as nearly as possible with a micrometer scale, and the results tabulated on a basis of 100 (table I). The number of days intervening between each observation are given as well as the total gain and average gain per day; x implies cutting was a failure; + signifies width at least as much as given; ? indicates apparent loss due to local growth fluctuation.

The table is of value in leading us to certain general conclusions. On May 13, the width of the new-formed ring was greatest in cuttings 4–6. It gradually dwindled in size toward the apical shoot, while below there appeared to be a decline followed by an increase. The next investigation was made on May 25, twelve days later.

TABLE I

No.	Amount	Amount	No. of days	Gain	Gain per day	Amount	No. of days	Gain	Gain per day	Amount	No. of days	Gain	Gain per day
	May 13, '09	May 29, '09				June 3, '09				June 15, '09			
1	3	5	12	2	0.17	5	9	0	0.00	35	12	30	2.50
2	3	5	12	2	0.17	20	9	15	1.63	25+	12	5	0.42
3	8	8	12	0	0.00	24	9	16	1.78	x	12	x	x
4	12	15	12	3	0.25	40	9	25	2.78	35	12	?	?
5	12	18	12	6	0.50	30	9	12	1.33	40	12	10	0.83
6	12	20	12	8	0.67	30	9	10	1.11	35	12	5	0.42
7	8	13	12	5	0.42	40	9	27	3	40	12	0	0.00
8	x	10	12	x	x	30	9	20	2.22	38	12	8	0.67
9	8	11	12	3	0.25	40	9	29	3.22	45	12	5	0.42
10	6	10	12	4	0.34	21	9	11	1.22	30	12	9	0.75
11	x	x	12	x	x	25	9	x	x	42	12	17	1.42
12	11	8	12	?	x	x	9	x	x	17	12	x	x

Looking at the average gain per day, we see that in cutting 6 the greatest increase occurred, while above and below the amount of gain varied irregularly with the different cuttings. However, the gain in the apical shoot was but slight. Comparing the results of May 25 with those of June 3, it is evident that, with the exception of the apical shoot, the average daily increase at the latter date was greater in every case than in the former. In other words, the tree grew faster in diameter, with the exception of the terminal shoot, during the last of May and the first of June than before that time. It follows from the table that the rate of increase varies considerably with the cutting and obeys no general law. The data of June 15, however, are most interesting. There was a decrease in the rate of growth between June 3 and June 15, with the exception of the apical shoot. Here, on the contrary, the gain in 12 days was 15 times as great as that of all the diameter growth previous to June 3. There was then a very marked increase in the formation of the annual ring at this point as compared with the gradual decrease in the remainder of the tree. Unfortunately, however, data are not available bearing on the rate of elongation of the apical shoot. It would appear, however, that its elongation must have been very rapid up to June 3, so much so in fact that the increase in the width of the annual ring could not result. From June 3 to June 15 the rate of elongation probably decreased appre-

ciably, while greater increase of wood formation resulted as a natural sequence.

Before summing up the results of the preceding paragraph, some observation on cessation of cambial activity should be given. It has long been recognized that while cambial activity makes itself manifest in many trees at about the same time, there is no relation evident in its cessation. Thus BUCKHOUT (**2**) found in *Larix decidua* that there was little if any growth after July, while *Pinus Strobus* continued to form wood until well into September. R. HARTIG (**6, 7**) also gives data bearing on this subject. In beech it lasts 2.5 months, in oak 4 months, in Scotch pine and Norway spruce 3 months. FRIEDRICH (see WIELER **14**), on the contrary, claims that in coniferous and hard woods in general there are two periods of growth, one lasting until about the end of May, sinking until the middle of June, and reaching a maximum again in July. Complete cessation resulted by the middle of August. The majority of workers, however, unite with HARTIG in saying that cessation of cambial activity varies greatly with the species concerned.

In the present studies, the latest cuttings in 1909 were made on July 6 upon tree III. At that time growth was still in progress throughout. Comparing these with cuttings taken from the same tree on February 21 of the next year, the following interesting results are obtained. Cutting 2 showed 0.5 of the ring complete, cutting 4, 0.6, cutting 8, 0.85. R. HARTIG (**6**) agrees with T. HARTIG (**8**) that cessation of growth begins first in the crown in trees in open stand and proceeds gradually downward. If such is the case, the data just given present an anomaly, or else growth was accelerated in the apical portions after June 15. However some of HARTIG'S data are in accordance with that already given. For example (BÜSGEN **3**), on June 21 the ring of an oak as compared to that of a previous year gave the following data:

At 1.3 m. height.....0.45 complete
At 3.5 m. height.....0.45 complete
At 5.7 m. height.....0.45 complete
At 7.9 m. height.....0.72 complete
At 12.3 m. height.....0.57 complete
At 14.5 m. height.....0.56 complete (3–4 year branch)

HARTIG then obtained results comparable to the present ones; that is, at about the middle of June he observed that growth was most advanced near the middle of the tree and decreased in both directions from that point. And yet he persists in his assertion that growth ceases in trees in open stand first in the youngest branches. Such being the case, the only possible solution of the data given above is that there must have been a marked acceleration of growth in the apical portions after June 21 and a corresponding decrease in the parts below. Whether the same applies in the pitch pine further investigation must decide. There was an increase in radial growth in the apical shoot and at the same time a decrease below between June 3 and 15, but that growth ceased first above cannot be deduced from the present observations.

As regards the theory advanced by FRIEDRICH concerning two periods of maximum growth in trees, little can be said. The second period if present in *Pinus rigida* must be the minor one, inasmuch as the ring was on an average more than half completed on June 15.

Width of the ring

Measurements were made from sections of tree III to determine the width of the ring at different heights. According to HARTIG, in trees in open stand the amount of wood formed increases from apex to base. This may arise from one of two alternatives; either the annual ring may decrease in size owing to the increasing diameter, or the reverse may be true. The latter, he says, is but rarely the case and sometimes occurs in trees which are exceptionally well nourished, that is, those possessing a large vigorous crown. From these observations it is to be expected that in *Pinus rigida* the ring would increase perceptibly in width toward the base, inasmuch as the crown is as a rule not exceptionally well developed. Such was the case. At cuttings 1 and 4, the completed ring on February 21, 1910, was about the same width. At cutting 8 it was but 0.85 the size of that above, while cutting 12 showed a still further decrease to 0.70. It follows that in *Pinus rigida*, if there is such a decrease in the size of the ring from apex downward in young vigorous growing trees, the same applies with even greater force in older trees with longer axis and poorly developed crown.

The living portion of the cortex, on the contrary, follows a law exactly the reverse. In the upper portions of the crown the cortex is necessarily thin, inasmuch as it contains a relatively small series of bast parenchyma and sieve tube areas. Below, the thickness of the cortex increases markedly, so much so in fact that it often attains 3–5 cm. in width. The storing capacity of the cortex as a result must be greatest in the basal portions of the trunk. Assuming that food abundance alone was concerned in cambial awakening, the latter would result first below. Inasmuch as it does not, there are certainly other determining factors, chief among which is probably insolation.

Investigations on the older trees revealed a number of factors of sufficient interest to demand mention in this paper. A curious feature long known to former workers was especially prevalent. I refer to the often noted lessened density of the wood on the south side of trees. This is due to the fact that the proportion of summer wood on the north side is greater as compared with the width of the ring than on the south side. This disparity in wood formation, however, is not so marked in young individuals. The ring formation is much more regular and it is only in the older trees that the phenomenon above described is seen. As to the cause of this lessened density on the south side, no reasonable conclusion was attained in these investigations, nor has it ever been satisfactorily accounted for. It is without doubt correlated with insolation in some way, but further study is necessary to determine this definitely.

The manner of cambial awakening likewise presents an interesting study. It was observed that even on different sides of the same section a noticeable disparity often occurred. In some cases growth had proceeded to the extent of one or two partly formed tracheids, while in closely neighboring spots the cambium appeared as yet in the resting condition. Nor was one tracheid completely formed as to size before another began. Often rows of three or four small tracheids were visible, none of which had yet attained half the size of those formed first the previous year. In such cases it would appear that cell division was so rapid in the cambial region during favorable seasons that new elements were laid down before

their predecessors had yet attained their maximum size and strength.

Double rings were often in evidence in the old trees. These might easily cause miscalculation as to age. The phenomenon of double ring formation has often been observed, especially in broad-leaved trees. Here it was ascribed sometimes to partial or complete defoliation, at others to favorable or unfavorable external factors. The first assumption would not hold in *Pinus rigida* in this case or in general, since defoliation rarely occurs. The cause must be ascribed to external growth conditions, but what these are would be difficult to determine. That they are most prevalent in old trees is well known, and this would lead one to infer that their formation is in some manner correlated with inhibition of growth, since the effects of this are most marked on older less vigorous individuals.

Secondary thickening in the roots

Little stress was put on the study of secondary root thickening in the present investigation. Only one cutting was taken, on April 27, 1910, for purposes of comparison, so that no reliable deductions can be made. At this time cambial activity was not manifest, although it must have been in process throughout the aerial portion with the possible exception of the apical shoot. T. HARTIG (**8**) claimed that cambial awakening in the roots is much later than in the aerial portions. He gave midsummer as the time of first inception and said it continued far into October. Whether the same applies to *Pinus rigida* further investigation only can decide. Suffice it to say, however, that the growth in thickness of roots must not be confused with growth in length. The latter is manifest often as early as March and continues throughout the season.

Summary

1. The histological characters of *Pinus rigida* present no wide variation from the normal coniferous type.

2. The secondary thickening in the root is similar to that in the stem, but differs (*a*) in less sharp demarcation between the annual rings, (*b*) in the biseriate character of tracheids, and (*c*) in less density.

3. Growth began in young 20–30-year old specimens of *Pinus rigida* in the vicinity of Ithaca as early as April 15. While there was no direct evidence of cambial awakening secured the previous year, sections taken at a later date showed growth in such an advanced state that it must have begun fully as early.

4. In older trees cambial awakening is sometimes retarded at the base where proper insolation is lacking.

5. There is no appreciable difference in the time of cambial awakening on the north and south sides of trees.

6. Growth began first in 20–25-year-old specimens at some distance below the apical shoot, but during a period of 19 days gradually spread upward until it reached the apex of the trees.

7. Investigations on trees *A*, *B*, and *C* tend to show that growth in older individuals begins first in the crown and spreads downward. The time of its inception at the base varies with conditions of insolation, bark, etc.

8. Growth in the branches follows the same rule as in the main axis. The time of awakening in the former is almost if not absolutely identical with that in the latter.

9. Growth spreads down the main axis faster than it does along the lateral shoots.

10. Except in the terminal shoot, growth in diameter was more rapid between May 25 and June 6. In the terminal shoot itself greatest rapidity of growth was manifested between June 6 and June 15.

11. No reliable deductions concerning cessation of cambial activity can be drawn from the present investigations.

12. The width of the complete ring decreases from apex to base; the living portion of the cortex follows the reverse rule.

13. A number of peculiarities already noted by others are prevalent in mature specimens. These are (*a*) lessened density of wood on the south side of trees, (*b*) irregularity of cambial awakening in closely neighboring parts of the same section, (*c*) successive formation of new elements before previous ones have reached their maximum size, and (*d*) double rings.

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EXPLANATION OF PLATES XXIV AND XXV

FIG. 1.—Cutting taken from apical shoot of tree III April 15, 1910; cambium in the resting condition; ×50.

FIG. 2.—Same, but cutting taken about 1 m. from the apex; cambium in the resting condition; ×50.

FIG. 3.—Same, but cutting taken about 2 m. from the apex; growth in evidence to the extent of one or two partly formed tracheids; ×50.

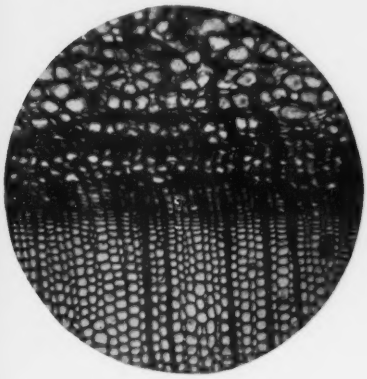
FIG. 4.—Cutting taken from apical shoot of tree III May 4, 1910; growth just beginning at *A;* compare with fig. 1; ×50.

FIG. 5.—Same, but cutting taken 1 m. from the apex; growth slightly more advanced; compare with fig. 2; ×50.

FIG. 6.—Same, but cutting taken from the apex; growth in evidence to the amount of 3 or 4 tracheids; compare with fig. 3; ×50.

FIG. 7.—Cutting taken from tree III April 15, 1910, about 3 m. from the apex; growth in evidence to the extent of one or two partly formed tracheids; ×50.

FIG. 8.—Same, but cutting taken about 4 m. from the apex; growth in evidence to about the same extent as in fig. 7; ×50.



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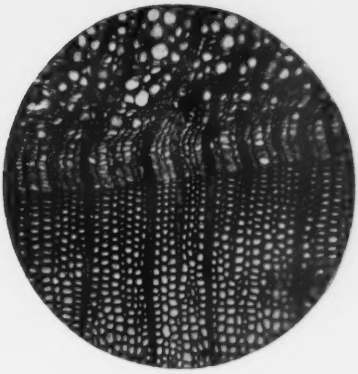

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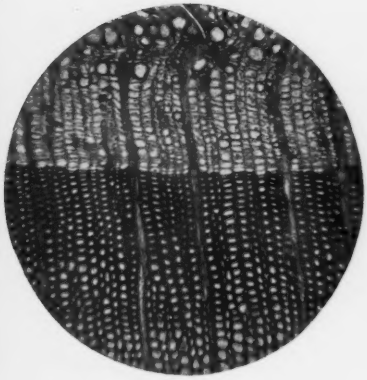

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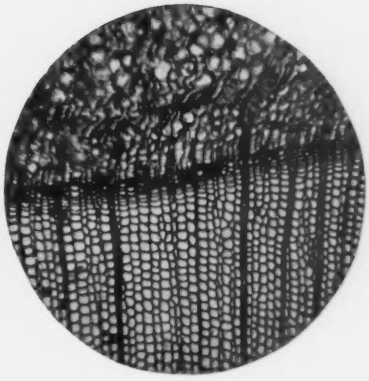

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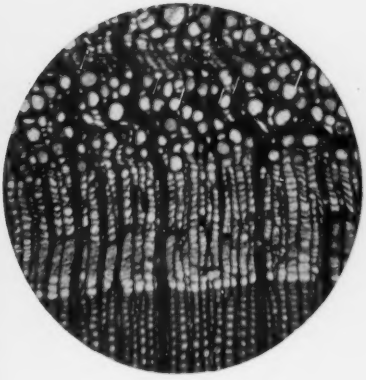

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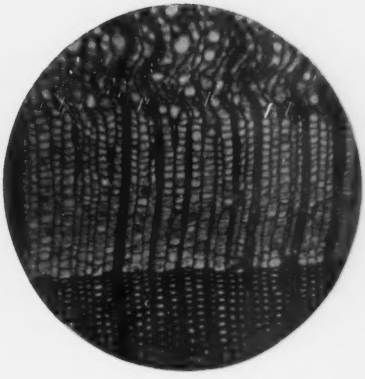

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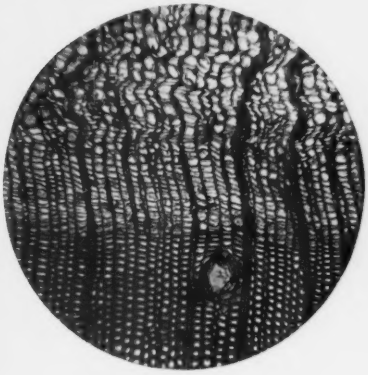
BROWN on PINUS RIGIDA



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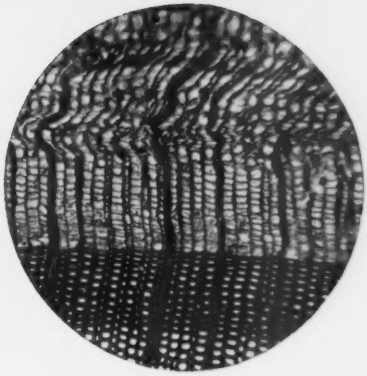

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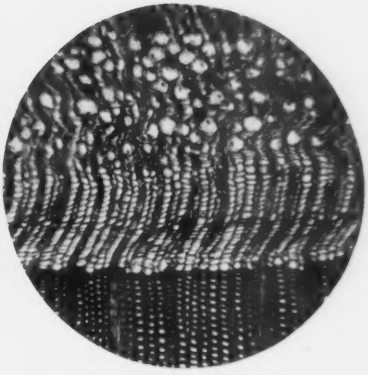

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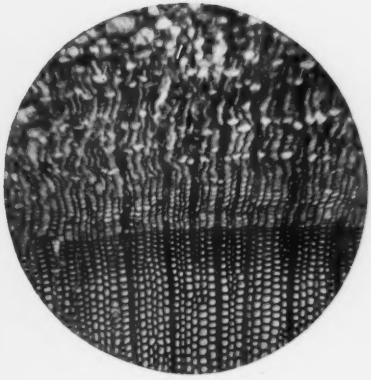

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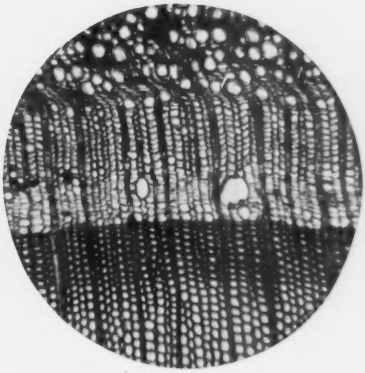

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BROWN on PINUS RIGIDA

FIG. 9.—Same, but cutting taken about 5 m. from the apex; cambium in the resting condition; ×50.

FIG. 10.—Cutting from main axis of tree VI April 22, 1910, at a distance of 3 m. from the apex; growth in evidence to the extent of several rows of partially formed tracheids; ×50.

FIG. 11.—Same, but cutting from the base of a lateral branch which entered the main axis 20 cm. below cutting shown in fig. 10; no growth in evidence; ×50.

FIG. 12.—Same, but cutting taken 40 cm. below that in fig. 10; growth in evidence to the extent of several rows of tracheids; ×50.

CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. XII

NEW PLANTS FROM IDAHO

AVEN NELSON

In this paper are continued the studies upon the plants of southern and western Idaho, begun in no. IX of this series of Contributions. As stated in the preceding paper, the present studies are based upon collections made in 1911, largely by Mr. J. FRANCIS MACBRIDE, but assisted in the field for a time by the writer. There are also included in this paper a few species based upon collections made by Miss JUNE A. CLARK, of Boise, at present a student in the Idaho State University. During 1911 she made very creditable collections of the plants of the mountains adjacent to Boise, and in the mountains of Washington County of her state.

Melica Macbridei V. H. Rowland, n. sp.—A green slender erect tufted perennial, 2–5 dm. high, growing from bulbs, which may be solitary or in clusters of 2–6: culms and sheaths (which exceed the internodes) hispid-scabrous on the prominent nerves: leaves exceeding the sheaths in length, usually 3 in number, the basal withering early, flat, thin, and weakly ascending, 1–4 mm. wide: panicle loosely open; rachis decreasingly scabrous toward the apex, with 3–9 nodes, the first internode 3.5–5 cm. long: rays 1–3 at each node of the rachis, if 3, the first subsessile, the second on a short pedicel, the third on a long capillary reflexed pedicel: spikelets 2–5-flowered, 7–13 mm. long, with terminal flower sterile, never flattened: glumes unequal, herbaceous, scarious-margined, quite often purple-tipped, oblong, acute; the first 4 mm. long, 3-nerved and about two-thirds as long as the second; the second 5-nerved, 6 mm. long: lemma thicker than and about equaling the second glume, lightly scabrous throughout, obtusely bifid: palet reaching to the notch in the lemma, 2-keeled, spathe-shaped with the lower part inclosing the white wormlike rachilla, ciliate on the keels from near the middle to the apex: fruit cylindrical with the divergent styles sometimes persistent.

This species is nearest to *Melica bromoides* Gray, from which it differs as follows: *M. Macbridei* is about one-half as high as *M. bromoides* and much slenderer and more graceful in appearance; it is much more scabrous and the roughness continues beneath the sheaths to very near the nodes of the culm; the sheaths exceed the internodes; the floral parts are shorter and wider than in *M. bromoides;* the nerves of the glumes and lemmas never extend to the margins; and lastly the rachilla between the flowers is smooth, white, and "wormlike" and never green as in the other.

This is number 948 of MACBRIDE'S 1911 collection of Idaho plants, secured on dry slopes at Silver City, June 20.

Calochortus umbellatus, n. sp.—Bulb small, ovoid to subglobose: stems slender, 3–5 dm. high, 2–3-leaved; lower leaf long, 4–8 mm. wide, from one-half to three-fourths as long as the stem; the other leaves narrowly linear (if only one, near the middle), 5–10 cm. long: flowers 3–9, in an umbel; pedicels slender, erect (in a fascicle), 5–10 cm. long; involucral bracts few–several, 2–4 cm. long, the ovate base scarious, abruptly narrowed to the long filiform green acumination: sepals lanceolate, acuminate, one margin more broadly scarious than the other, 25 mm. or less long: petals obovate-cuneate, the rounded summit more or less erose and abruptly apiculate or subacute, white, with an indigo or purple spot near the middle; the gland small, round, yellow, short-setose, some long soft filamentous hairs scattered over the lower half of the petal: filaments not much if any longer than the anthers, dilating gradually from apex to base: capsule ellipsoidal, about 15 mm. long, narrowly thin-winged, lightly transversely striate.

There is no doubt that this has passed as *C. nitidus* Dougl., to which it is closely related. The Idaho specimens seen by the writer cannot, however, well be so referred. PURDY has recharacterized *C. nitidus* in his excellent revision (Proc. Cal. Acad. Sci. III. **2**:128. 1901) and the following facts, drawn from his description are in direct contrast with *C. umbellatus:* "Stems *bulb-bearing* near base, *not* bracted in the middle"; "umbel of 2–4 flowers subtended by *2–4* linear bracts"; "sepals *ovate-lanceolate, exceeding* the petals"; "petals *2 inches* long, the *same* in width"; "filaments *filiform,* winged *below*"; capsule strongly winged and *crested.*"

NELSON and MACBRIDE'S no. 1197, July 19, 1911, is taken as the type. The species seemed quite abundant on sagebrush lands near Wood River at Ketchum. Mr. C. N. WOODS has also secured it (no. 258) in the same county (Blaine). A specimen from Yellowstone Park by Mrs. E. W. SCHEUBER is also referable here.

Zygadenus salinus, n. sp.—Bulbs globose, or even depressed globose, not deep-set (4–8 cm.), 1–3 cm. in diameter; outer bulb-coats brown, thin, and fragile; the next succeeding ones delicately thin-scarious, glistening white: leaves green, grasslike, usually folded, scabrous on the margins, somewhat pruinose, especially on the greenish sheaths, 7–12 mm. broad, shorter than the scapose stems: stems slender, erect, 3–6 dm. high, with 2–3 non-sheathing linear leaves: raceme short, rather crowded; the pedicels slender, becoming 2–3 cm. long; the bracts with short ovate base and very long linear acumination, the lower as long as or longer than the pedicels: flowers in a simple raceme, yellowish-white; perianth segments nearly similar, 3–7-nerved, all clawed; the sepals with very short claw, ovate, obtuse; the petals elliptic, obtuse, with evident claw which is more or less concave or inrolled; the glands in both small, inconspicuous, and confined almost wholly to the upper part of the claw: stamens surpassing the perianth, on filaments only slightly dilated below: ovary free from the calyx; the styles 2–3 mm. long: fruit ovate, about 6 mm. long; the cells united to the summit.

I should hesitate to describe this as a new species were it not for the globose bulbs and the habitat. The near allies are *Z. venenosus* Wats. and *Z. intermedius* Rydb. These have elongated bulbs; the former has conspicuous glands, and the latter has all the leaves with scarious sheathing base. Both have deep-set bulbs, and belong to dry non-saline soil, while the proposed species was secured in alkali-bog lands, with the bulb but a few centimeters below the surface. It seems that typical *Z. venenosus* is confined to the coast states (see PIPER'S Fl. Wash. 198, and BLANKINSHIP, Mont. Science Studies 1:45).

Type no. 889, MACBRIDE, Emmett, June 9, 1911.

Salix boiseana, n. sp.—A low shrub, forming clumps, 1–2 m. high: twigs glabrous, reddish brown or chestnut, slightly shining or obscurely glaucous: leaves oblong, either obtuse or subacute at apex, usually cuneately narrowed at base, 2–4 cm. long, minutely pubescent but green above, pale with a fine tomentum beneath, margin quite entire; stipules wanting: pistillate aments with two or three foliar bracts at base, 3–5 cm. long: floral bracts (scales) small, ovate, obtuse and brown, about half as long as the pedicels, long silky hairy below, especially near the apex and margin, gla-

brate above: pedicels slender, 1.5–2 mm. long; capsules glabrous, 3–4 mm. long: style evident but very short (less than 0.5 mm.).

This is most nearly allied to *S. Wolfii* Bebb, but seems to be distinct by the cuneate base of the leaves, which are glabrous or nearly so above, tomentose on the lower face (not silky-villous with shining hairs on both sides), by the longer pedicels, the slenderly virgate fertile stems (*S. Wolfii* is freely short-branched), and the longer fertile aments. *S. boiseana* belongs to lower altitudes and matures much earlier in the season.

Miss JUNE CLARK secured the type material (no. 48) in overripe condition, May 29, 1911, near Boise at an altitude of less than 3000 feet.

Eriogonum fasciculifolium, n. sp.—The shrubby base low (1–2 dm.) and somewhat di- or trichotomously branched; the more or less scaly bark dark brown or dirty black: leaves fasciculate or verticillate on the enlarged nodes, mostly on the crownlike apex of the branchlets, linear or narrowly oblanceolate, 1–3 cm. long, tapering to a short petiole, rather thick, pale-green, glabrate above, obscurely tomentose below: peduncles from the upper nodes or terminal, 4–8 cm. long, bearing a few-rayed umbel, lightly pubescent; the bracts foliar, apparently always few (2–4), or sometimes wanting: rays 12–20 mm. long: involucre many-flowered, campanulate, its ovate-oblong reflexed lobes as long as the tube, sparsely silky-villous: flowers pale yellowish-white, rather large: sepals similar, broadly obovate, about 5 mm. long, lightly silky-villous below and on the pedicel to the joint: filaments pubescent below, much shorter than the triangular glabrous achene.

This new member of § PSEUDO-UMBELLATA is at once distinguished by its branched shrubby base and its very narrow leaves, though it has all of the characteristics of the section.

A limited quantity only was secured by Miss JUNE CLARK at Tamarack, Washington County, Idaho, August 12, 1911, no. 236, on a dry mountain side.

Stellaria (ALSINE) **praecox,** n. sp.—A diminutive vernal species of arid districts: stems usually simple but sometimes branched from the base, glabrous except for some crisped hairs on the lower internodes, 7–15 cm. high (including the long filiform pedicels): leaves few, mostly in a basal rosette, with 1 or 2 pairs on the lower part of the nearly filiform stem, narrowly lance-linear, 5–12 mm. long: cyme unequally 3-rayed, some of the rays again unequally trichotomous; the bracts minute, somewhat scarious: sepals

lanceolate, scarious-margined, about 3–5 mm. long: petals wanting: stamens 5, opposite the sepals and less than half as long: stigmas 3, nearly sessile: capsule ellipsoidal, each of its 3 valves 2-toothed, shorter than the calyx; seeds several.

Some of its characters are suggestive of *S. umbellata* Turcz. (*Alsine baicalensis* Coville). That also is apetalous and has five stamens, but in it they alternate with the sepals. The capsule is oblong-ovoid and twice as long as the sepals. The seeds in the two seem nearly identical, with an almost annular embryo. The aspect of the two species of course is wholly different, *S. praecox* looking more like a very slender *S. longipes* Goldie.

The plant has added interest because many of the scarcely distorted capsules were found to be filled with a smut which Dr. CLINTON pronounces as new also, and to which he has given the name *Ustilago Stellariae*.

MACBRIDE secured this at Falk's Store, Canyon County, Idaho, on moist slopes, under sagebrush, no. 763, April 24, 1911.

Crataegus tennowana, n. sp.—Small treelike shrubs, 3–6 m. high, sometimes growing in clumps and then lower and less treelike: trunk short, usually less than 1 dm. in diameter: spines straight, nearly at right angles, lustrous reddish-brown becoming grayish, about 15 mm. long (1–2 cm.): leaves mostly oval (varying to suborbicular) in general outline, both base and apex with rounded contour, often however cuneately narrowed below and more rarely above as well; the upper half from shallowly to deeply and irregularly serrate, the teeth with more or fewer gland-tipped serrulations; the lower half glandular serrulate or with a few sessile glands on the entire margins (occasionally the glands extend down upon the petiole which is only 2–10 mm. long); pubescence wanting from the first upon the petioles and on the underside of the leaves, sparsely and minutely hirsute on the upper side, especially along the veins, from the first to maturity; the veins of the rather thin leaves somewhat superficial on the lower side, the midrib flattened and narrowly wing-margined, at least in the young leaves: corymb wholly glabrous except for a slight pubescence on the inner face of the calyx lobes, 5–15-flowered, with scattering glands on the peduncle and pedicels and very rarely on the triangular-lanceolate persistent calyx lobes: stamens seemingly 8 when the styles and carpels are 4, and 10 when the styles and

carpels are 5 (the more unusual number); anthers pink: fruit black or purplish-black, maturing in July: carpels with rounded back, cuneately narrowed to the somewhat sulcate ventral angle, not narrowed at base.

This may be thought too near *C. Douglasii* Lindl., but authors are fairly well agreed that that species should have the following characters, to none of which this seems to attain:

Tree size (30–40 feet high, with trunk sometimes as much as 20 inches in diameter): leaves ovate to obovate, with cuneate base, densely pubescent above, on the veins below, and on the petioles when young: calyx lobes deciduous, glandular serrate: stamens 20 (SARGENT), 10–20 (BRITTON, ROBINSON, and FERNALD, *et al.*): anthers yellow: styles surrounded at the base with long pale hairs: fruit ripening in August and September: carpels narrowed at base.

In view of the differences indicated it would seem that at least some of the western forms that have heretofore passed as *C. Douglasii* need to be separated from it.

The type is MACBRIDE'S no. 799 (flowers, May 10; ripe fruit, from naked tree, July 8), moist woods, Falk's Store, Canyon County.

Trifolium tropicum, n. sp.—Apparently green and glabrous but under a lens pubescent with scattering white hairs, especially near the midrib both above and below: stems single, from slender rootstocks, erect, slender, 2–3 dm. high: leaflets linear, 3–6 cm. long, 2–5 mm. wide, minutely denticulate by the projection of the beautifully arcuate nerves; petioles slender, from much shorter to much longer than the leaflets; stipules linear, the free portion usually denticulate, 14–18 mm. long, either shorter or longer than the adnate portions: heads about 2 cm. high, nearly as broad, solitary or 1 or 2 smaller ones from the upper leaf-axils, in bud silvery-silky with the long abundant hairs on the filiform calyx lobes: flowers purple to rose-red, soon reflexed and nearly concealing the pubescence of the calyx: calyx lobes longer than the thin scarious glabrate tube: standard oblong, with rounded apiculate apex, about 10 mm. long and 4 mm. broad when spread out flat; wings as long as the standard, the blade narrowly oblong, conspicuously auricled at base, as long as the slender claw; keel petals semi-oval, shorter than the wings, the claw longer than the blade: style a little longer than the stamens: ovary glabrous, about 8-ovuled.

Most nearly allied to *T. Harneyensis* Howell, from which it is at once separated by its pubescent leaves, sessile flowers (which are early, not tardily, reflexed), and glabrous calyx tube and ovary.

MACBRIDE'S no. 967, from Jordan Valley, Owyhee County, in moist loam soil, June 22, 1911, is the type.

Lupinus tenuispicus, n. sp.—Silvery-silky, with loose, copious, somewhat spreading and tangled hairs: perennial, in dense clumps on a woody caudex, 3–7 dm. high: stems rather slender, sparingly branched: radical leaves on slender petioles 1–2 dm. long; leaflets 6–9, narrowly oblanceolate or nearly linear, 4–6 cm. long; cauline leaves similar, shorter-petioled and (above) sessile: spikes slender, crowded, 5–15 cm. long: bracts small, linear-lanceolate, somewhat shorter than the nearly sessile calyx: calyx barely gibbous at base, about 5 mm. long: flowers blue: standard nearly orbicular, the blade pubescent on the back with fine long hairs (only visible under a good lens), 6–8 mm. long, sharply emarginate at apex; wing petals oval, on very short claws; keel petals small and delicate, the blade semi-ovate, on a claw half as long: pods very short, 1–3-seeded, pubescence as on the rest of the plant.

I can find no described species in this range having the very slender and crowded spikes, the small apparently glabrous petals, and the short few-seeded (often only one) pods of this form.

No. 203, by Miss JUNE CLARK, from Tamarack, in the mountains of Washington County, Idaho, August 8, 1911, is the type.

Astragalus nudisiliquus, n. sp.—Habit and appearance of *A. utahensis* T. & G., the white indument even thicker and more felted: caudex woody and freely branched: pod about 20 mm. long, probably at first white woolly-hirsute, the indument at length deciduous and disclosing the longitudinal striae, coriaceous-woody, ovoid, flattened dorsally, the acute apex abruptly flexed, the dorsal suture slightly keeled, the ventral somewhat sulcate.

When the writer collected this and first examined it later, he took it for granted that it was merely an over mature *A. utahensis*. On noting the character of the pod, however, it is evident that this is not the case. In that species the indument is permanent, both sutures are inflexed, the body of the pod is smaller, the apex is essentially straight, and, as a more strikingly characteristic difference, the striae are transverse. In view of these facts it seems best to put this species (which has no doubt passed for *A. utahensis*) on record.

Secured by NELSON and MACBRIDE on the steep cobblestone bluffs of the Snake River, at King Hill, Idaho, July 15, 1911, no 1088.

Astragalus obfalcatus, n. sp.—The woody taproot vertical, with an enlarged crown, or in older plants with closely branched caudex, the branches with enlarged crowns: stems solitary or few from the crown or crowns, stoutish, erect, coarsely striate, green and glabrate or sparsely hirsute with white hairs, few-leaved, 1–3 dm. high: leaves crowded on the crowns, somewhat spreading upon the nearly erect petioles (the dead petioles persisting), canescent with straight stiffish widely spreading coarse hairs; leaflets 7–13, from oblong (or spatulate) to elliptic or obovate, 10–20 mm. long; petioles 5–10 cm. long, those of the stem shorter: peduncles axillary, few-flowered: calyx tube 5–7 mm. long, the pubescence on it mostly finer and shorter, black in part, its linear lobes nearly as long as its tube: bracts linear, rarely as long as the calyx tube: pods widely divaricate, falcate upward, abruptly long-cuspidate, canescent with coarse hairs, completely 2-celled by the intrusion of the dorsal suture, the rounded back scarcely sulcate, somewhat flattened laterally to the almost carinate ventral edge, the stout stipe not as long as the calyx tube: seeds many.

In habit this species suggests *A. mollissimus* Torr. The shape of the leaflets and even the pubescence is somewhat similar, and the pod is 2-celled, but there the similarity ends. There are a few other species in which the pods are falcate upward, but *A. obfalcatus* approaches none of these as closely as it does *A. mollissimus*.

Secured by MACBRIDE (no. 1023) in dry lava soil, on Reynolds Creek, in Owyhee County, July 3, 1911 (full fruit; flowers not seen), and by NELSON and MACBRIDE (no. 1119), at King Hill, in loose lava cinders, July 15, 1911.

Lathyrus Bradfieldianus, n. sp.—Glabrous, mostly less than 1 m. high, stems weakly erect, among undershrub which give partial support, rather strongly striate but noticeably angled only on the more or less branched upper portion: leaflets mostly 10, subsessile, beautifully and rather strongly veined, bright green above, scarcely paler beneath, from broadly elliptic and obtuse (or even retuse) to narrowly ovate and acute, all subulate-tipped, 15–30 mm. long; tendrils well developed, somewhat branched; rachis moderately stout, the petiolar part usually shorter than the

internodes; stipules large, consisting of a triangular-lanceolate upper portion (which is entire and acute, or somewhat acuminate) and a much larger somewhat reniformly expanded basal part (which is usually coarsely and irregularly 3–5-toothed): flowers large, 3–8, closely approximated at the end of the long (10–15 cm.) axillary peduncles: calyx very oblique, the lanceolate teeth small, each shorter than the part of the tube to which it is attached, except the lower one which is linear and nearly as long as the tube: petals dark blue or purplish, lighter toward the base; the claw of the standard rather broad, sulcately folded and with conspicuous winglike crests at junction with abruptly flexed or reflexed reniform or orbicular emarginate blade; wings broadly elliptic, on a very slender claw shorter than the blade: pods nearly straight, 5–6 cm. or more long, 6–8 mm. broad, about 15-ovuled.

Resembling and related to *L. pauciflorus* Fernald, BOT. GAZ. **19**:335, 1894, from which it is readily distinguished by its broad obtuse lower leaflets, its stipules with their remarkably expanded bases, its more numerous and larger and broader flowers, and always by the conspicuous rounded crownlike crests at the summit of the folded claw.

MACBRIDE'S no. 927, from Silver City, on brush covered hills, June 19, 1911, is the type. Mr. WILLIAM C. CUSICK'S no. 2538, from mountains near North Pine Creek, Oregon, is to be referred here, as well as Miss CLARK'S no. 85, from Boise (Clear Creek), July 4, 1911. The species is named in honor of Mr. A. D. BRADFIELD, superintendent of the Silver City schools, an appreciative student of his local flora, who spent much time in the field assisting Mr. MACBRIDE.

Viola Clarkae, n. sp.—Perennial from a woody sub-horizontal rather long rootstock, which bears a simple or branched caudex: branches of the caudex 1–4 cm. long, brown, and rough with the old petiolar bases: new plants often arising from the nodes of the rootstock at intervals of 2–5 cm.: herbage glabrous: stemless, or stems long (2–3 dm.), weak and procumbent and bearing several normal leaves: leaves mostly on the crowns of the caudex, crowded; the petioles very slender, 3–10 cm. long; the blade ovate, 2–5 cm. long, tapering rather gradually from near the base to the obtusish apex, the base roundish and shallowly cordate, the margin obscurely crenate and smooth; stipules greenish, linear, with few-many filiform pinnately arranged lobes or teeth: peduncles filiform, about

as long as the petioles, or if borne on the stems nearly as long as the whole of the subtending leaf: flowers (at least the late ones) rather small, blue: sepals lance-linear, less than half as long as the petals: lateral petals broadly spatulate, about 1 cm. long, a circular spot near one margin (toward the base) covered with rather long stiff white hairs; lower petals obovate, emarginate, 15–18 mm. long (including the straight spur with its abruptly bent acute tip): stigma obscurely pubescent: capsule smooth: seeds brown, with a pale conspicuous strophiole-like attachment.

There seems to be no near relative of this among the western species of *Viola*.

I have pleasure in dedicating this apparently strong species to Miss JUNE CLARK, of Boise, Idaho, who made an extensive collection of the plants, in duplicate, in her home neighborhood and in the mountains of Washington County, during the season of 1911. Her no. 84, from Clear Creek, in the Boise Mountains, July 4, 1911, is the type.

CHRYSOTHAMNUS OREOPHILUS **artus,** n. var.—Differing from the species in the stricter, narrowly racemose panicle, the filiform semi-cylindrical leaves, and the more glutinous involucres.

Secured by Miss CLARK, near Boise, September 1, 1911, no. 317. Collected also by HENDERSON at Nampa, July 30, 1897, and by CUSICK in Eastern Oregon, September 7, 1900, no. 2503. Distributed by them as an unnamed variety of *C. graveolens*.

CHRYSOTHAMNUS PUMILUS **latus,** n. var.—Distinguished from the species by the thin, flat, broad leaves (5–8 mm. wide) and the small cymose corymbs.

Were one to see just the herbage of this plant, it might readily be mistaken for some *Chrysopsis*.

NELSON and MACBRIDE'S no. 1236, Ketchum, Idaho, July 20, 1911, is typical. Certain numbers by other collectors seem to be more or less intermediate.

ERIGERON FILIFOLIUS **Bloomeri,** n. comb.—*E. Bloomeri* Gray, Proc. Am. Acad. **6**:540. 1865; *E. fissuricola* A. Nels. in Herb.—Perhaps no better example has been afforded of that form of error which comes from founding a species upon a single collection, or even upon several, when those represent a mere fraction of the range of the plant as it later comes to be known, than is supplied by what we now know of *E. filifolius* and its near allies. Whether this

liability of making a mistake, because of lack of knowledge of the variability and range of the plant in hand, is so grave a matter that one ought to be deterred altogether from founding a species upon a single collection may well be questioned. No doubt there are those who would take the affirmative, but general adherence to such a practice is manifestly impossible and probably also undesirable. To begin with, it would bar out the amateurs and amateurs are the stuff out of which professionals (experts) are made. It would defer publication of even the best of species, often indefinitely, and that is to kill interest and delay development. There would be little incentive to make collections were it understood that some one in the next generation would make report upon all except the well known things. That it is desirable to avoid the making of useless synonyms cannot be too strongly emphasized, but even a few synonyms is to be preferred to stagnation and death.

Nevertheless, such an array as the following ought to secure renewed caution in the best of us and deep penitence in the worst of us. Those who lament (and that includes the "chiefest sinners") are prone to think that great facility (perhaps agility) in making synonyms is peculiar to the present generation. Let us see how these examples (scores of others, just as illuminating might be found) bear out that idea.

DOUGLAS collected two plants in the region of the Columbia which were described in HOOKER'S *Flora* (**2**:20. 1834) as *Diplopappus filifolius* and *D. linearis*. The first of these NUTTALL transferred, and it became *Erigeron filifolius* (Trans. Am. Phil. Soc. **7**:328. 1841), although he probably did not himself know the plant, since the canescent paniculately branched stems and the yellow flowers mentioned by him do not belong together. In the meantime DECANDOLLE had based another name upon the same Douglasian collection, viz. *Chrysopsis canescens* (Prodr. **5**:328. 1836), and in spite of the fact that he speaks of the flowers as yellow, the chances are that this name refers to *Diplopappus linearis*, at least in part, just as NUTTALL'S name does. In the TORREY and GRAY *Flora* (**2**:177. 1842) this difficulty is not cleared up, but the true facts are suggested, in part, while they are also obscured by the retention of NUTTALL'S *E. ochroleucum* (*loc. cit.*), to which HOOKER'S

D. linearis is referred. Following this, apparently not much is gained by the publication of *E. pumilus* Hook. (Lond. Journ. Bot. **6**:242), nor the new combination (*E. canescens* Parry [Jones Exp.], no. 239), for GRAY refers both of these also to *E. ochroleucum*. GRAY in the *Synoptical Flora* (**1**:213. 1884) continues the confusion that had been increased by the publication of *E. peucephyllus* (Proc. Am. Acad. **16**:89. 1880), in which characters belonging in part to both of HOOKER'S species are combined.

These facts have been recited merely to show the impossibility of foreseeing the degree of variation or even the direction in which it will tend; hence the synonyms. Incidentally it shows that synonyms are inseparable from any period of great botanical activity, even when the work is in the hands of such veritable princes in systematic work as HOOKER, NUTTALL, TORREY, GRAY, and PARRY.

In 1865, GRAY published *E. Bloomeri* (Proc. Am. Acad. **6**: 540). Taking the material then available he was more than justified. It has taken nearly half a century of additional exploration to lead any one to question its validity. It happened that the first specimens of it represented it in its most depauperate stage, from the arid mountains of Nevada. Subsequent collections greatly extend its range, and a series of specimens leading straight into typical *E. filifolius* is now at hand, and may no doubt be duplicated in many of the larger herbaria. Even its raylessness is not an infallible character. MACBRIDE secured at Silver City, on a stony hilltop, a series of specimens that, if sorted and reported upon by one not familiar with their history, would appear as *E. Bloomeri* (rayless) and *E. filifolius* (radiate). These grew intermingled and were intentionally collected together and placed together upon the sheets to emphasize that fact. Under the circumstances one may even wonder why retain the name at all, but in view of the marked differences between the extremes in the series, perhaps the name had best stand varietally for the rayless forms.

In COULTER and NELSON'S *New Manual of Botany* (p. 527), the opinion is expressed that *E. curvifolius* Piper, Bull. Torr. Bot. Club **27**:396. 1900, is the same as *E. luteus* A. Nels., Bull. Torr. Bot. Club **27**:33. 1899. More careful scrutiny indicates that that opinion

was not well founded. The *Chrysopsis hirtella* DC. Prodr. 5:327. 1836, upon which PIPER's species was based, has a characteristic pubescence that separates it from *E. luteus* and *E. filifolius* as well. Since, however, there is nothing but its pubescence to separate it from the latter, it may as well become

ERIGERON FILIFOLIUS **curvifolius,** n. comb.

The status of *E. luteus* A. Nels (*loc. cit.*) cannot yet be passed upon with certainty. So far only the type collections are available, and these show some characteristics of habit and habitat that may denote its distinctness. If it is ever reduced it will be to separate varietal rank under *E. filifolius*.

ERIGERON COMPOSITUS **breviradiatus,** n. var.—Tufted on the crown of a solitary taproot, nearly glabrous: peduncles stouter and heads larger and broader than in the species: rays white to pale blue, broad, shorter than the disk flowers and barely surpassing the involucral bracts.

E. compositus Pursh already has more described varieties than it needs (see COULTER and NELSON, *New Manual*, p. 528), but the form here characterized is so unique that it needs to be catalogued in some way.

Secured by MACBRIDE at Silver City, June 17, 1911, no. 899.

Cordylanthus (ADENOSTEGIA) **bicolor,** n. sp.—Pilose throughout, with gland-tipped, subviscid hairs: stems mostly simple at base, rather freely branched upward, 3–5 dm. high: leaves 2–5 cm. long, linear and entire, or pinnately 3–5-divided; lateral lobes much shorter than the terminal, widely divaricate: heads terminating the branchlets, mostly 3 or 4-flowered, subtended by 4–6 foliar trifid bracts as along as or surpassing the flowers: calyx purple or purplish, diphyllous, the upper sepal 2-nerved, bifid, 10–12 mm. long; the lower oblong and entire, 3-nerved below, 5-nerved above, as long as or longer than the corolla: corolla purple, tipped with bright yellow, about 15 mm. long; the two lips equal, both appearing as if entire, but the lower with a rounded obtuse apex, the sides infolded and with an ovate tooth longer than the middle lobe; the sinuses plicate and having two thin lanceolate teeth: stamens 2; the anthers 1-celled, pubescent at both base and apex, the second cell represented by a pubescent rudiment, attached to the filament just below the fertile one; filament flattened and

with a U-shaped curve near the top: the stigma on the thickened inflexed tip of the style just protruding from the orifice of the folded galea-tip: capsule elliptic-oblong, few-ovuled, 4–6 maturing.

That this has passed for *C. capitatus* Nutt. seems quite probable. That it is in reality quite distinct the following differences indicate conclusively. No authentic specimens of *C. capitatus* are at hand, but it does not seem probable that NUTTALL, GRAY, WATSON, and others have all overlooked or that they would have been silent on the following points: the glandulosity; prevalence of pinnatifid leaves even below; the open panicle branching (not fasciculate-capitate); the bracts in excess of the flowers in the head; the unequal calyx leaves; the inflexed lateral lobes of the lower lip of the corolla; the laciniate plicae in its sinuses; the curved filaments and the rudimentary anther cell; and the beautiful purple of the flowers emphasized by the yellow, pubescent corolla tips.

Secured by NELSON and MACBRIDE on moist sagebrush slopes, at Ketchum, Blaine Co., July 20, 1911, no. 1239 (type); MACBRIDE, at Pinehurst, August 17, 1911, no. 1671.

Pentstemon brevis, n. sp.—Densely matted in tufts few–several dm. in diameter: roots woody, numerous, intricately interwoven: stems very numerous, borne on the crowns of the short slender subterranean branches of the caudex, usually 5–8 cm. high, though sometimes higher, very minutely puberulent as are also the leaves: leaves entire, moderately thick; the lower from oblong-elliptic to oblanceolate or spatulate, obtuse or subacute, 5–10 mm. long, tapering to a petiole often as long; stem leaves becoming sessile and narrower: inflorescence a narrow glandular-pubescent thyrse: calyx cleft into broadly lanceolate lobes 3 mm. or less long, rather thick and green except near the base: corolla dark-blue, slender, nearly tubular, 6–8 mm. long, bilabiate, with short rounded lobes and with short yellow pubescence in the throat and on the sterile filament: anthers dehiscent from the base and confluent but not explanate.

This species reminds one, in its low densely matted habit, of *P. caespitosus* Nutt., but in other respects it is more suggestive of a diminutive *P. humilis* Nutt. No one seeing these three species in the field, or even in dried specimens, will doubt their distinctness. *P. brevis* is alpine on wind swept summits.

NELSON and MACBRIDE, no. 1457, Lemhi Forest, Mackay, Custer County, Idaho, July 31, 1911. The only other specimen, seen by the writer, that approaches this species is CUSICK'S no. 1974, from bleak summits of Stein's

Mountains, E. Oregon, distributed as *P. humilis*, but which it is not. CUSICK'S specimen is larger in every way and less leafy on the stems.

Artemisia potens, n. sp.—Growing in small dense patches, the nearly simple virgate stems each from a long horizontal rootstock: stems rather slender, pale-green, slightly striate, minutely puberulent, 4–8 dm. high: leaves 3–6 cm. long, pale-green and glabrate above, thinly tomentose below, the margins revolute, simple or pinnatifid, the few (2–4) divaricate lobes and the body linear or nearly so: panicle narrow, dense, 7–15 cm. long: heads numerous, subspherical, 2–3 mm. high: involucral bracts oblong to oval, with greenish center, nearly glabrous, the delicately scarious margins appearing as if obscurely fringed: bracts linear, 1 or 2 to each cluster of 3–6 heads, longer than the heads they subtend and often nearly as long as the cluster: flowers 20 (more or fewer), the marginal ones pistillate, the inner perfect, all fertile: achenes glabrous.

In floral characters this is near *A. discolor* Dougl., but the aspect is that of *A. aromatica* A. Nels. or *A. redolens* Gray. In *A. potens* the heads form a long compact panicle and are as nearly erect as their crowded condition will permit. *A. discolor* has a woody caudex; *A. potens* is herbaceous to the ground. *A. discolor* grows in the moist rich soil of the mountains; *A. potens* on the dry saline-gravelly clays of the plains. The name refers to the overpowering but wholly characteristic *Artemisia* odor.

Type from Mackay, July 30, 1911, no. 1413, by NELSON and MACBRIDE.

UNIVERSITY OF WYOMING
LARAMIE, WYOMING

TWO SPECIES OF BOWENIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 162

CHARLES J. CHAMBERLAIN

(WITH FOUR FIGURES)

All the cycads except *Bowenia* have pinnate leaves, so that bipinnate leaves make *Bowenia* a very unique genus. It is found only in Australia, and even there is limited to Queensland, ranging from the northern part of the state to about the latitude of Rockhampton, in the Tropic of Capricorn.

Bowenia is described as monotypic, with *B. spectabilis* as the only species, although taxonomists recognize a var. *serrata*, which is often called *serrulata*.

B. spectabilis is found in the northern part of the range. I found it at Babinda, near Cairns, and followed it for some distance toward Innesfail, where it was said to be fairly abundant. Mr. J. H. BAILEY, director of the Brisbane Botanical Garden, told me that it is abundant at Cooktown; others, not professional botanists, claimed to have seen it much farther north.

B. spectabilis var. *serrata*[1] is so abundant in the Maryvale and Byfield region near Rockhampton that it forms a dense, but easily penetrated underbrush in the prevailing *Eucalyptus* bush. Mr. R. SIMMONS, of Rockhampton, gave me directions for reaching this *Bowenia* locality. I studied the variety for a distance of 20 miles and did not see a single plant resembling the species. Similarly in the Babinda region I had not seen a single specimen which could have been mistaken for the variety. In fact, the differences between the two are so pronounced that they should be regarded as distinct species.

[1] **Bowenia serrulata** (André) Chamberlain, n. comb.—*B. spectabilis* Hook. f. var. *serrulata* André, Ill. Hort. **26**: 184. *pl. 366* (1879); *B. spectabilis* var. *serrata* Bailey, Queensland Flora 1507 (1902).—Caudex subterraneus sphaericus supra multicaulis; caulibus caespitosis 1–2 m. altis; foliolis serratis.—Vicinity of Rockhampton, Queensland.

Whether the margin of a leaflet is entire or serrate or spinulose may be trivial in some cases and important in others, even within the range of a single family. *Dioon spinulosum* was for a long time characterized almost solely by the spinulose leaflets, but the character is so constant that determinations based only upon this feature are quite safe. On the other hand, the leaflets of the African *Stangeria paradoxa* may show the entire or the serrate character on the same plant or even on the same leaf. In the Botanical

FIG. 1.—*Bowenia spectabilis* at Babinda, Australia: about 1 m. in height

Garden at Durban, South Africa, Mr. WYLIE showed me a plant of *Stangeria paradoxa* with leaflets so deeply incised that the leaves might almost be called bipinnate. In *Stangeria* the character is so fluctuating that it is of no taxonomic importance. In some species of *Encephalartos* the fluctuating variations in the margins of leaflets have doubtless led taxonomists into pitfalls.

In *Bowenia* the serrate or entire character of the margin is so constant that it would be worthy of specific rank even if it were not

correlated with the difference in geographical distribution and other features.

As found in nature, the species and the variety are noticeably different, the latter having a greater display of foliage (figs. 1 and 2). The species is most abundant in open places and clearings, while the variety is most abundant in the bush. Many specimens of the species in shaded places along streams are larger and taller than forms growing in the open, the leaves sometimes reaching a length

FIG. 2.—*Bowenia serrulata* at Byfield, Australia: about 1.3 m. in height

of nearly 2 m., while those in the open seldom exceed a meter in length, but the leaflets of plants growing in the shade never become spinulose. The leaves of the variety range from 1 to 2 m. in height, with about 1.3 m. as the prevailing size. The leaves are dark green, very glossy, and they retain their beauty for a long time, especially in the species, some leaves of which, after lying for three days on a veranda in the blazing tropical sun of Babinda, still looked almost as fresh as when taken from the plant. The sub-

terranean stem has a remarkably tenacious hold on life. Mr. EDWARD MEILLAND, who lives in the *Bowenia* region, told me that a stem just beneath the beaten path under the house had not produced a leaf for 20 years, but when the old house was abandoned and the path no longer used, the stem, so long dormant, produced a fine display of foliage.

The most striking difference between the species and the variety is in the stem, which is subterranean in both. In the species the stem is somewhat carrot-shaped, with one or two, sometimes four or five, slender branches at the top (fig. 3). These slender branches bear all the leaves and cones.

FIG. 3.—*Bowenia spectabilis:* a somewhat diagrammatic sketch of the stem of an ovulate plant; the portion shown is somewhat less than 1 m. in length; the dotted line is the ground line.

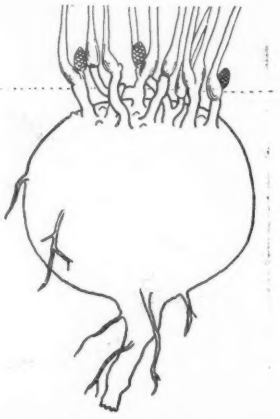

FIG. 4.—*Bowenia serrulata:* a somewhat diagrammatic sketch of the stem of a staminate plant; the stem is about 23 cm. in diameter; the dotted line is the ground line.

Sometimes they extend to the surface, but generally the bases of the leaves and the lower third of the cone are covered by the soil. Root tubercles are present but are generally 10–20 cm. below the surface.

In the variety the stem is spherical or turnip-shaped, usually about the size of a man's head, and has 5–20 slender branches at the top, like those of the species, only more numerous and reaching to the surface or even a little above (fig. 4). The slender branches themselves often branch. As a consequence, the foliage display is much greater in the variety than in the species. Usually, the slender branch bears only one leaf at a time, but two or three leaves are sometimes present. Cones are borne only on the slender branches.

In both species and variety the slender branches arise from buds at the top of the main stem, the buds often being due to injuries. Where the main stem has been torn by the plow, numerous buds may start.

Considering the difference in geographical distribution, the difference in leaflets, and particularly the striking difference in the stems, I have suggested that the variety be elevated to specific rank. I have had the assistance of my colleague, Professor J. M. GREENMAN, in the preparation of the description.

UNIVERSITY OF CHICAGO

BRIEFER ARTICLES

A NEW SPECIES OF ANDROPOGON

Andropogon urbanianus, n. sp.—Perennis; culmis glabris, 60–120 cm. altis; laminis teretibus, glabris; racemis binis, 2–4 cm. longis, vagina longioribus; rachi villoso; spicula sessili glabra, a basi villosa, 5 mm. longa, arista 2 cm. longa; pedicelli sterili villoso, 5 mm. longo, spicula pedicellata 3 mm. longa.

Perennial; culms glabrous, 60–120 cm. high, branched above, sheaths villous on the margin and toward the summit, or glabrate; ligule membranaceous, ciliate, 2 mm. long; blades terete, channeled above, glabrous, the two margins of the channel scabrous, villous above at base, 10–20 cm. long, about 1 mm. thick, tapering to a fine point; racemes 2 from each sheath, silky but not densely so, 2–4 cm. long, scattered along the upper part of the culms, usually of unequal length, the rachis joints slender, villous with long hairs, the subtending sheath shorter than the racemes; sessile spikelets 5 mm. long, glabrous, villous at base, scabrous above on nerves and keels, the awn geniculate, twisted below, 2 cm. long; sterile pedicel about as long as sessile spikelet, villous with hairs as much as 1 cm. long; pediceled spikelet reduced to a scale 3 mm. long.

Type specimen collected in Santo Domingo, Prov. Barahona near Las Salinas, by Padre MIGUEL FUERTES, no 1420, Sept. 1911. Other specimens referred to this species are: CAMACHE (St. Michel), Haiti, "in prato montano sicco"; W. BUCH no. 1074; FURCY, Buch 961.—A. S. HITCHCOCK, *Washington, D.C.*

EVAPORATION AND THE STRATIFICATION OF VEGETATION

(WITH ONE FIGURE)

During some investigations of the evaporating power of the air in various plant associations, data were obtained that show the amount of increase in the atmospheric humidity of the confined area of a ravine, and that tend to emphasize the contention of YAPP[1] that the varying

[1] YAPP, R. H., On stratification in the vegetation of a marsh, and its relations to evaporation and temperature. Ann. Botany **23**:275–320. 1909.

evaporation conditions at different levels in the same plant association may permit plants to grow in close proximity with one another, and yet, vegetating principally in different strata, to be subject to rather widely different growth conditions. Evidence supporting this view has also been furnished by DACHNOWSKI[2] and SHERFF[3] from observations extending over comparatively brief periods, all of these observers working in swamp or bog habitats.

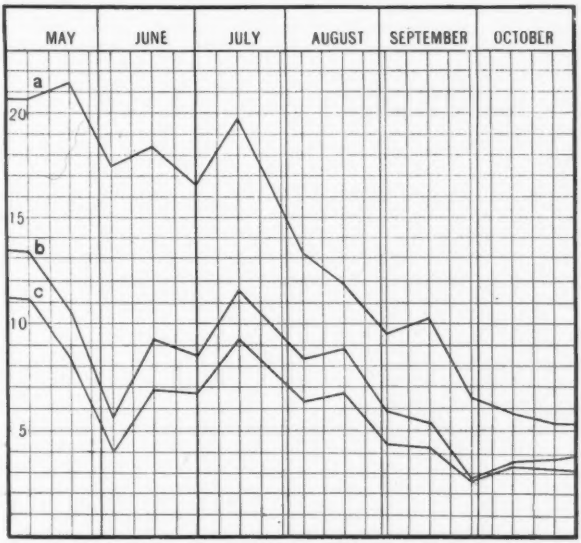

FIG. 1.—Diagram showing the average daily rate of evaporation in three strata of the beech-maple forest association for the growing season of 1911.

The present records were obtained during the season extending from May 1 to October 31, 1911, in some comparatively undisturbed beech-maple forests about 45 miles southeast of Chicago near the little village of Otis, Ind. The forest was of the usual climax mesophytic type. Its vegetation and the methods employed in obtaining the evaporation data by the use of the LIVINGSTON atmometers have been described in a

[2] DACHNOWSKI, A., Vegetation of Cranberry Island. BOT. GAZ. **52**:126–149. 1911.

[3] SHERFF, E. E., Vegetation of Skokie Marsh. BOT. GAZ. **53**:415–435. 1912.

previous paper.[4] The observations were made and the results have been plotted graphically for three different strata, with the intervals between the weekly readings as abscissae and the daily evaporation from the standard LIVINGSTON atmometer as ordinates (fig. 1). The intermediate graph (fig. 1*b*) represents the mean of three stations situated upon the forest floor, with the atmometers 25 cm. above the surface of the soil, in conditions of average vegetation. Here the average rate for the season was 7.4 cc. per day. The highest rate (fig. 1*a*) is that given by an instrument elevated 2 m. above the forest floor and shows an average of 13.5 cc. daily, or very nearly twice the amount of the stations immediately above the soil surface. The third record (fig. 1*c*) is for a station situated upon the slope of a ravine 10 m. deep, cut in the clay soil by a wet weather stream, and having a V-shaped outline in cross-section. The atmometer was placed 4 m. below the edge of the ravine and gave an average for the season of 5.9 cc. daily.

If the average rate of evaporation at the stations upon the forest floor be taken as unity, the proportional evaporating power of the air in the three strata will be found to be very nearly 1.84:1.00:0.80 for the season, and these figures may be taken to represent, more exactly than any previously available data, the measure of the mesophytism of these three several regions. It may also be noted that the elevated station has a much higher rate proportionally during the first half of the season.

The object of this paper being to indicate the amount of difference existing in the atmospheric conditions of some of the different strata of the same association, and to show how these differences may vary throughout the growing season, no attempt will be made to relate the vegetation to the different rates of evaporation. More extensive records must be obtained and an intensive study of the composition of the association undertaken before any satisfactory conclusions can be reached. It is interesting and important, however, to note the different atmospheric conditions to be encountered by forest tree seedlings during the first two years of their existence and at a later period when they reach the height of a meter or more. This may indicate one of the most important reasons why so many of the beech seedlings die before attaining the height of two meters. It may also be remarked that the lower evaporation in the ravine may be a sufficient explanation for the presence upon its slopes of a much greater abundance of such delicate forms as *Dicentra canadensis*, *D. Cucullaria*, *Impatiens biflora*, and *Asplenium angustifolium*.—GEORGE D. FULLER, *University of Chicago*.

[4] FULLER, G. D., Evaporation and plant succession. BOT. GAZ. **52**: 193–208. 1911.

CURRENT LITERATURE

MINOR NOTICES

Das Pflanzenreich.[1]—Part 46 is a monograph of the Menispermaceae by Professor LUDWIG DIELS. The author devotes about 45 pages to a general consideration of the family and then establishes 8 tribes which are based largely on the presence or absence of albumen and the character of the endocarp. These 8 tribes embrace 63 genera and 357 species; and approximately one-fifth of the total number of species are new to science. Two new genera are added, namely *Platytinospora*, based on *Tinospora Buchholzii* Engl. of tropical Africa, and *Sinomenium*, based on *Cocculus diversifolius* Miq. of Asiatic distribution.

Part 47 continues the monographic treatment of the Euphorbiaceae by Professor FERDINAND PAX, including only the tribe CLUYTIEAE. The author divides the tribe into four subtribes, namely CODIAEINAE, RICINODENDRINAE, CLUYTIINAE, and GALEARIINAE, depending on the number of stamens and the free or united petals. The tribe embraces 24 genera and about 150 species, 22 of which are new to science. One new monotypic genus (*Uranthera* Pax & Hoffm.) is proposed from the Malayan Peninsula. This part also includes an elaboration of the Cephalotaceae by Professor J. M. MACFARLANE. Only one monotypic genus of this family is known at the present time, namely *Cephalotus* from West Australia.

Part 48 continues the monographic treatment of the Araceae by Professor A. ENGLER, and contains the subfamily LASIOIDEAE to which are referred 18 genera and upward of 130 species, 18 of which are here published for the first time. One new genus (*Dracontioides*) is described, based on *Urospatha dehiscens* Schott of southern Brazil. *Amorphophallus* is by far the largest genus, being represented by about 75 species or more than one-half the total number recorded for the entire subfamily. Numerous and excellent illustrations amplify the text.

Part 49 contains a supplement to the Monimiaceae by Dr. JANET PERKINS, and records the results of a continued study of this family from new material represented in the leading European herbaria, particularly the Berlin herbarium

[1] ENGLER, A., Das Pflanzenreich. Heft 46 (IV. 94). Menispermaceae von L. DIELS. pp. 345. *figs.* 93 (917). 1910. *M* 17.40. Heft 47 (IV. 147. iii). Euphorbiaceae-Cluytieae, unter Mitwirkung von KÄTHE HOFFMANN, von F. PAX. pp. 124. *figs.* 35 (144); (IV. 116). Cephalotaceae von J. M. MACFARLANE. pp. 15. *figs.* 4 (24). 1911. *M* 7.20. Heft 48 (IV. 23C). Araceae-Lasioideae, von A. ENGLER. pp. 130. *figs.* 44 (415). 1911. *M* 6.60. Heft 49 (IV. 101. Nachträge). Monimiaceae (Nachträge) von J. PERKINS. pp. 67. *figs.* 15 (112). 1911. *M* 3.60. Leipzig: Wilhelm Englemann.

through the rich collections of WEBERBAUER and ULE from South America and of MOSZKOWSKI, RÖMER, and SCHLECHTER from New Guinea and New Caledonia. Important data concerning older or little known species are recorded, and more than 30 species new to science are added to the monograph of this family by the same author, published in the *Pflanzenreich* in 1901. One new genus is proposed, namely *Carnegiea* from New Caledonia. All species enumerated are referred to in such a manner that the supplement can be used readily and advantageously with the *Monograph* itself.—J. M. GREENMAN.

The slime molds.—The second edition of LISTER's *Mycetozoa*[2] is a notable contribution to our knowledge of these much discussed organisms. The new book follows the principal lines of the first edition, but has been improved and enlarged throughout. Six genera and 70 species have been added, so that the group now contains 49 genera with 246 species. The plates in the first edition were splendid, but those of the present volume are even better, and rank with the best illustrations which have ever been published of any plant structures.

Miss LISTER was constantly associated with her father in the preparation of the first volume, and the present work, published four years after his death, shows that she is able not only to make excellent illustrations, but also to organize and add to the text. It is distinctly a joint publication.

The "passing" of the slime molds is not referred to, the designation "organisms" being used in all cases, so that the title *Mycetozoa* is the only indication that the authors might be inclined to regard the organisms as animals rather than as plants. Until some decisive evidence appears, there is no reason for removing the specimens from the herbarium or for changing the library catalogues.—CHARLES J. CHAMBERLAIN.

Handbook of deciduous trees.—In 1904 SCHNEIDER's *Handbuch* began to appear, and at the completion of the first volume (1906) it was reviewed in this journal.[3] Since that time the six parts constituting the second volume have appeared at intervals, and have been noted. Now the work has been completed with the appearance of the twelfth part and the general index.[4] As stated in preceding notices, it contains descriptions, with illustrations, of the angiospermous trees of central Europe, both native and under cultivation. The final part completes the dicotyledons (*Fraxinus* to *Metaplexis*), contains

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[2] LISTER, ARTHUR, and LISTER, GULIELMA, A monograph of the Mycetozoa, a descriptive catalogue of the species in the herbarium of the British Museum. 8vo. pp. 1–302. *pls. 201. figs. 56.* London: Printed by order of the Trustees of the British Museum. 1912.

[3] BOT. GAZ. **43**:43:214. 1907.

[4] SCHNEIDER, C. K., Illustriertes Handbuch der Laubholzkunde. Zwölfte Lieferung. Imp. 8vo. pp. 817–1070. *figs.* 515–628. Jena: Gustav Fischer. 1911. *M* 5. Also Register. pp. vii+138. *M* 5.

the monocotyledons (*Yucca* to *Agave*), and also an extensive supplement (pp. 869–1065) to all the preceding parts.—J. M. C.

North American flora.[5]—Volume **17,** part 2, contains the Poaceae (in part) from the genus *Arthraxon* to *Paspalum* by GEORGE VALENTINE NASH. One new genus is proposed, namely *Schaffnerella*, based on *Schaffnera gracilis* Benth. from Mexico. Several transfers are made, and new species are described in the following genera: *Schizachyrium* (4), *Andropogon* (1), *Amphilophis* (1), *Sorghastrum* (1), *Aegopogon* (2), and *Paspalum* (6).—J. M. GREENMAN.

NOTES FOR STUDENTS

Cytology of Polytrichum.—What is to be regarded as the first critical work on the cytology of mosses appears in a recent number of *Archiv für Zellforschung*. ALLEN[6] has studied and described with great care the structure and division of the antheridial cells of *Polytrichum*. For the sake of accuracy he finds it advisable to introduce several new terms: the cells which are to be metamorphosed into spermatozoids are referred to as *androcytes*, those of the penultimate generation as *androcyte mother cells*, and those of all the earlier generations as *androgones*.

In all androgones a deeply staining kinoplasmic mass is present in the cytoplasm; in the earlier generations it has the form of a large plate, while in the later generations it usually exists as a group of smaller bodies or "kinetosomes." All transitions between the two conditions are found. Previous to mitosis, the plate divides to two daughter plates, or in the case of the kinetosomes into two daughter groups, which move apart and occupy positions at opposite sides of the nucleus. Before the division of the plate a few achromatic fibers connect it with the nuclear membrane, and when the divergence of the daughter plates is complete these have increased greatly in number, determining the position and extent of the future broad-poled spindle. In the cells with kinetosomes there are no fibers discernible until the migrating groups reach their final positions. The spindle at length includes connecting fibers, mantle fibers, and usually a few short, freely ending ones.

The resting nucleus contains a single deeply staining mass made up of both nucleolar material and chromatin, and a sparse reticulum composed of chromatin and linin. As mitosis approaches, the nucleus enlarges until its membrane touches the polar plates or kinetosomes, while the material of the reticulum forms a spirem which segments into chromosomes. The presence of nucleoli at this stage offers additional evidence that the chromatin and nucleolar substance are distinct. The nucleus now collapses and the chromatin

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[5] North American flora, vol. **17,** part 2, pp. 99–196. New York Botanical Garden. September 18, 1912.

[6] ALLEN, C. E., Cell structure, growth, and division in the antheridium of *Polytrichum juniperinum* Willd. Archiv für Zellforschung **8**: 121–188. *pls. 6–9.* 1912.

becomes compacted into a tight knot. Soon the six chromosomes, all U-shaped and closely similar, disentangle themselves from this knot and become arranged on the spindle. They split longitudinally, separate, and reorganize the daughter nuclei in the usual way. During the anaphases and telophases the connecting fibers between the chromosome groups increase in number, pull away from the chromosomes, and become thickened at their ends. These thickenings apparently move toward each other and meet in the equatorial region, where by further swelling of the fibers the cell plate is formed. The splitting of the cell plate and the deposition of a wall between its halves were not observed, but are believed to occur.

In the androcyte mother cells there are a few granules, but nothing which can be certainly identified with the kinetosomes, whose bulk has been diminishing through the generations of androgones. There is, however, in each of them a small "central body" at the center of an aster in the cytoplasm. There is no evidence that it originates within the nucleus. It divides to two which diverge, each with an aster, to opposite sides of the nucleus. Some of the astral rays form cones whose bases are at the nuclear membrane, but between the separating daughter centers there is visible no constant connection. The central bodies are located at the sharp poles of the spindle, and as the nucleus swells it comes in contact with them. Although they are less conspicuous from this time on, it is reasonably certain that they persist in every instance through mitosis, which is essentially similar to that in the androgones. In the cytoplasm of each androcyte is a deeply staining granule occupying the position of the pole of the former spindle. This is the blepharoplast and is doubtless identical with the central body of the androcyte mother cell. The development of the spermatozoid is to be taken up in a later paper.

The spermatogenous cells are marked by a condition of polarity which persists throughout the life of each cell and is transmitted through a long series of cell generations. Except during mitosis, there is no trace of a polar arrangement of the nuclear structures.

The kinetosomes are believed to be not comparable to "chondriosomes" or other non-kinoplasmic inclusions of the cytoplasm. They are not definite morphological entities, but rather unorganized masses of reserve kinoplasm. The definite behavior of the plates in the early androgones is regarded as the result of the presence of a large amount of kinoplasm which tends to occupy a fairly definite position relative to the nucleus.

In contrast to the kinetosomes the blepharoplast is a definitely organized cell organ, and although the author believes that the question of its morphological nature is still an open one, he inclines toward the view that it is the homologue of a centrosome. This is strongly warranted by the centrosome-like behavior of the blepharoplasts in *Polytrichum*, with which he ventures to predict other bryophytes will be found to agree. The need of further researches among the Chlorophyceae for light on the origin of the blepharoplast is emphasized.

Although the mitosis in the antheridial cells of *Polytrichum* agrees in general with that in higher plants, certain peculiarities are pointed out which may prove to be of phylogenetic significance. Such are the delay in the preparation of the nucleus for division until after the formation of the spindle rudiment, the great swelling of the nucleus in one dimension during the prophases, the equatorial aggregation of the chromatin following the swelling, and the final shrinkage of the nucleus. It is yet too early to say whether any or all of these features are generally characteristic of mitosis in bryophytes, but many fragmentary observations make this appear quite possible.

The comprehensive review of cytological work in the bryophytes and the extensive list of literature brought together contribute much toward rendering this paper of the highest value to students of cytology.—LESTER W. SHARP.

Mallow rust.—In an elaborate paper ERIKSSON[7] gives the results of many years' investigations on the mallow rust, which, coming originally from South America, has been introduced into Europe, North America, and other countries. The work is replete with experiments and observations covering all phases of the biology and life history of this fungus, which presents peculiar features of interest, first, because in the countries into which it has been introduced it has spread to many plants not native in its original habitat, and second because, being one of the lepto-Uredinales whose teleutospores germinate at maturity, its manner of living from season to season has not been satisfactorily explained. It is in fact this latter phase of the subject which forms the pivot of ERIKSSON's investigation, and upon which he brings to bear the results of a vast amount of painstaking work.

The main contentions of ERIKSSON are that the fungus persists in the seed of infected plants in the form of a mycoplasma, and that it is disseminated chiefly by means of infected seed. The mass of experimental and observational data upon which he bases these contentions are briefly summarized here.

The historical data relating to the distribution of the fungus show that in many places it was first observed on plants grown from seed obtained from infected nurseries. The fungus is not spread to great distances by means of the sporidia. Wide dissemination is brought about by means of infected seeds or seedling plants containing the fungus in the mycoplasma stage. In plants grown from infected seeds the first outbreak of the disease occurs regularly when the plants are about three months old. This period is required for the mycoplasma to change into the filamentous stage and produce spore pustules. The pustules of the primary outbreak are very numerous and are uniformly scattered over the leaves of the young plant, while those of the

[7] ERIKSSON, J., Der Malvenrost (*Puccinia Malvacearum* Mont.), seine Verbreitung, Natur, und Entwickelungsgeschichte. Kungl. Svensk. Vetensk. Handl. **47**: 5–120. *pls. 6. figs. 18.* 1911. For summaries previously published by the author see Compt. Rend. **152**:1776–1779. 1911, and Centralbl. Bakt. **31**:93–95. 1911.

secondary infection from sporidia are localized in groups near the points of infection. Neither the mycelium nor the spores survive the winter in Sweden. The teleutospores of this rust are of two kinds, and although they are morphologically indistinguishable, they behave differently on germination. Those of one type produce promycelia and sporidia in the usual way, but those of the second type produce slender germ tubes, whose terminal portions break up into several independent cells or conidia. The sporidia put forth germ tubes, which, penetrating the epidermis, make their way through the epidermal cells either directly into the intercellular spaces or into the palisade cells, and thence into the intercellular spaces. New sori result from these infections in 8–15 days. The conidia germinate, so to speak, by pouring their content into the epidermal cells, from which it migrates into the palisade cells, and finally through the entire plant. No outer visible sign results from these infections. The protoplasm of the fungus enters into a state of symbiosis with that of the host, thus forming the mycoplasm. The seeds of such infected plants produce seedlings in which the latent fungus manifests itself by a general outbreak of sori over the entire plant when it is about three months old. The change of the mycoplasm into mycelium is similar to that process described by the author in former papers.

Two other papers published shortly before the appearance of ERIKSSON'S account treat briefly of the mallow rust. In the first of these TAUBENHAUS[8] describes the two modes of germination of teleutospores noted by ERIKSSON, but, unlike ERIKSSON, he finds that the "conidia" abjointed by some of the germ tubes produce sporidia like other promycelial cells. Furthermore, he finds that the fungus is carried through the winter both by hibernating mycelium and by teleutospores. In plants in protected places, the mycelium resulting from late infections appears to produce sori, which develop slowly during the winter and mature the following spring. Regarding the hibernation of teleutospores, TAUBENHAUS finds that the teleutospores formed late in the season seem to behave like those of a *micro-Puccinia*. Some of these he found capable of germination during the winter and spring. With the advance of the season, however, the time required for germination increased from 24 hours to 6 days. This observation is quite contrary to the experience of DIETEL, who found that the period required for the germination of the teleutospores of *Melampsora Larici Caprearum*, a form with hibernating teleutospores, decreased with the advance of the season. Young seedlings may be infected by teleutospores borne in sori on the carpels and involucral bracts. Thus the fungus is distributed by means of infected seed and pieces of involucral bracts mixed with the seed, although the embryo is not infected.

In the second paper DANDENO[9] gives brief additions to his formerly

[8] TAUBENHAUS, J. J., A contribution to our knowledge of the morphology and life history of *Puccinia Malvacearum* Mont. Phytopathology **1**:55–62. *pls. 3*. 1911.

[9] DANDENO, J. B., Further observations on the life history of *Puccinia Malvacearum*. Rep. Mich. Acad. Sci. **12**:91, 92. 1910.

published observations on the mallow rust. According to him the mycelium of the fungus lives through the winter in the stems and petioles of *Malva rotundifolia*, but the teleutospores do not survive the winter in Michigan.

Although ERIKSSON's observations have added many facts to those already known of the general biology of the mallow rust, his conclusion that the fungus lives through the winter only in the form of a mycoplasma in the seed or young plant is largely inferential, and one is inclined to give preference to the explanations of TAUBENHAUS and of DANDENO as less at variance with general experience than is the mystical mycoplasma.—H. HASSELBRING.

Germination.—The irregularity of the differences in rapidity and percentage of germination in the unlike seeds of heterocarpic plants under various conditions of germination, when the fruit and seed coats are left intact, is well shown in a lengthy paper by BECKER,[10] who studied in a rather superficial way the germination of 47 species of Compositae, several Cruciferae, and three Chenopodiaceae. Morphological position, the sexual condition of the flowers, darkness, temperature, increased and decreased oxygen pressure, nitric acid, and Knop's solution influence now disk seeds, now ray seeds, or both, or neither according to species, apparently without regularity. Age and possible sterility of the seeds are disturbing factors in the results. Most of the experiments were performed with fruit coats intact, but enough were removed to prove that the inclosing structures are largely responsible for these differences, which always become much less on removal of the fruit coat. These differences in germination do not, therefore, as ERNST and CORRENS assumed, rest on differences in the constitution of the embryos. This fact has been recognized here for some years, but has not been properly recognized abroad. Embryos of dimorphic seeds may and do differ, as the reviewer has shown[11] for *Xanthium;* but the differences due to embryos alone cannot be determined with seed coats left on the seeds. With *Axyris amaranthoides* BECKER does not get total failure of the round seeds to germinate, as did CROCKER[12] with seeds of this plant from our northwest, but merely a very low germination. This may be due to ecoiogical differences in the regions where the plants grow affecting the seed coats.

As to the influence of increased oxygen, BECKER finds that brief exposure of seeds brings about the same kind of response as continuous exposure to high oxygen pressures, and argues therefrom that it exerts a chemical stimulus upon the protoplasm of the embryo, rather than increases the respiration as CROCKER has suggested. BECKER does not tell us what is the difference

[10] BECKER, HANS, Über die Keimung verschiedener Früchte und Samen bei derselben Species. Inaug. Diss. pp. 7–129. 1912.

[11] SHULL, CHAS. A., The oxygen minimum and the germination of *Xanthium* seeds. BOT. GAZ. **52**:453–477. 1911.

[12] CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZ. **42**:265–291. 1906.

between increase of respiration and his postulated stimulus. I have recently shown that there is a difference in the demand for oxygen by the embryos of the dimorphic seeds of *Xanthium*, and that the embryos do not germinate unless the minimum oxygen need is supplied. It cannot be doubted in the case of *Xanthium* that the oxygen is respired, and that up to the point where oxygen ceases to be a limiting factor, respiration increases with increased oxygen supply. If the seed coat structures limit oxygen sufficiently, the same conditions would obtain in any germination where free oxygen is necessary. BECKER'S contention, therefore, seems to be without sufficient foundation, especially since he made no attempt to measure the intensity of respiration under the conditions of his experiments. The idea that oxygen is a stimulus which "releases the mechanism" of germination is a conception typical of the German school of stimulus physiologists. BECKER is therefore orthodox in his interpretation of the less obvious chemical and physical changes in the germination of seeds. The Germans seem to find it difficult to grasp BLACKMAN'S conception of limiting factors, and apply it to the problems of plant physiology; or perhaps they merely prefer to leave the ultimate chemical phenomena of life and growth veiled under the term stimulus, which admirably conceals our ignorance of the real processes.

A study of the physical characters of the inclosing structures of the Compositae should disclose the causes of the irregular behavior BECKER reports, and careful exact studies of the chemical processes in the germinating seeds will show in how far the embryos are responsible for any of the noted differences.—CHARLES A. SHULL.

Cecidology.—Among the recent important European publications are the following: A paper by RÜBSAAMEN[13] on the cecidia of Africa and Asia describes and figures 38 cecidia from Africa and 6 from Asia. These are grouped with reference to the host plants and assigned to genera only. Most of the figures are for the purpose of showing the gross anatomical characters of the galls.

A paper by PANTANELLI[14] on the *Acarus* cecidia of the vine describes both the hypertrophies and the parasites. It is well illustrated with photographs of the injuries, microphotographs showing structures of the cecidia, and line drawings of the parasites. The subject is treated primarily from the standpoint of plant pathology and includes a description of one new species (*Phyllocontes viticolus*) and an excellent bibliography.

A paper by PARIS and TROTTER[15] gives a very important chemical study of the well known European gall of *Neuroterus baccarum* and the unaffected

[13] RÜBSAAMEN, EW. H., Beiträge zur Kenntnis ausser-europäischer Zoocecidien. V. Gallen aus Africa und Asien. Marcellia **10**:100–132. 1911.

[14] PANTANELLI, E., L'Acariosi della vite. Marcellia **10**:133–150. 1911.

[15] PARIS, G., and TROTTER, A., Sui composti azotati nelle galle di *Neuroterus baccarum*. Marcellia **10**:150–159. 1911.

part of the foliage of the host plant. The analysis is interesting, but incomplete. The lengthy and well selected bibliography will be valuable for workers in biochemistry.

A paper by HOUARD[16] is subdivided into five parts as follows: (1) table of galls previously described, in which are listed 26 species with bibliography of each and grouped with reference to the host plants; (2) new observations upon the new galls of Tunis, in which the author gives brief discussions of 93 cecidia, some of which are assigned to genera only; these cecidia are also grouped with reference to the host plants; most of them are attributed to insects, one on *Moriandia cinerea* Cosson is caused by *Cystopus candidus*, one on *Olea europaea* L. is caused by *Bacillus olea* (Arc.) Trev., and a third is referred to as a fasciation without comment as to cause; (3) a very valuable bibliography on the zoocecidia of Tunis from 1894 to date; (4) a table of galls arranged with reference to host plants; (5) a table arranged with reference to the organisms causing the galls.

COSTERUS and SMITH[17] have represented a very interesting paper on tropical teratology. Malformations of 18 species (7 of which belong to the family Orchidaceae) are carefully described. These descriptions are far better than those frequently given in papers on teratology in that the relationships of the parts have been carefully worked out. No explanation is offered as to the cause of these peculiar structures.—MEL T. COOK.

Gas movements in plants.—It is a question of some interest whether static diffusion accounts for essentially all the gas exchanges of foliar intercellular systems or whether molar movement is also considerably involved. OHNO[18] has already shown how "hygro-diffusion" leads to such a molar extrusion of gas in the leaf of *Nelumbo nucifera*, and has explained the physics of the action. Now URSPRUNG[19] shows that the same process plays an important part in the gas movements in the leaves of *Nymphaea* and *Nuphar*. The first half of the article is devoted to a critical historical review of the work on *Nelumbo*. The conclusions reached agree with OHNO in all essential points, although that author has given the earlier literature a less critical consideration than is desirable. As URSPRUNG states, it has generally been believed that the observed gas exchanges and positive and negative pressures in the intercellular systems of *Nymphaea* and *Nuphar* are entirely determined by photosynthetic and respiratory activities. A mention of two of his experiments will show clearly that "hygro-diffusion" plays an important rôle in these forms.

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[16] HOUARD, C., Les Zoocédicies de la Tunisie. Marcellia **10**:160–184. 1912.

[17] COSTERUS, J. C., and SMITH, J. H., Studies in tropical teratology. Ann. Jard. Bot. Buitenzorg II. **9**:98–116. *pls. 5*. 1911.

[18] BOT. GAZ. **51**:310. 1911.

[19] URSPRUNG, A., Zur Kenntnis der Gasdiffusion in Pflanzen. Flora **104**:129–156. 1912.

If the cut end of a petiole of a leaf of *Nymphaea* is placed just beneath the water surface while the upper face of the leaf blade is in the air, gas of about the composition of the air continuously extrudes from the cut end of the petiole with pressures varying from 0 to 17 cm. of water, and in volumes amounting to several times that of the leaf in course of an hour. Both the pressure and rate of extrusion increase with a rise of the temperature of the leaf and with dryness of the air in contact with the upper surface of the blade, and ceases when the air over the blade is saturated or when the blade is immersed. By piercing the upper surface of the blade of *Nymphaea* just over the petiole repeatedly with a needle, turning up the margin of the blade, and supporting a little water over the punctures, a great extrusion of air can be demonstrated, increasing with the temperature of the leaf and with dryness of the air over the marginal region of the blade. This is almost identical with the main observations on *Nelumbo*, and is explained by the same physical principle. URSPRUNG believes that a considerable part of the gas exchange in leaves of water plants floating or borne above the water is brought about by "hygro-diffusion," but that it plays no considerable rôle in the gas exchange of land plants with their narrow intercellular systems, and of course no part in submerged leaves. The studies of OHNO and URSPRUNG now make possible a much more lucid statement of gas movements and pressures in the intercellular systems of plants than was formerly[20] the case.—WILLIAM CROCKER.

Cytology of rusts.—Investigations of the cytology of *Puccinia Falcariae* by DITTSCHLAG[21] and of *Endophyllum Sempervivi* by HOFFMANN[22] show that the sequence of nuclear phenomena in these forms agrees in its essential details with that of other rusts. Among the facts presented the following are of special interest. In *Puccinia Falcariae*, which is an autoecious form of the *Puccinopsis* type, the binucleate phase arises by the lateral fusion of the cells of a palisade-like layer differentiated near the lower middle of the young aecidium. Unlike the mode of origin of binucleate basal cells in the true aecidia of *Puccinia Poae* as described by BLACKMAN and FRASER, the mode of origin of these cells in *Puccinia Falcariae* resembles more nearly that usually observed in aecidia of the *Caeoma* type, in which the fertile cells are not overlaid with a mass of sterile tissue. Occasionally three cells fuse and thus trinucleate basal cells arise. Occasionally the basal cells branch and form more than one row of spores. Regarding the trichogyne-like cells observed by some investigators, the author states that the so-called sterile cells are not always present, but when they are they occur on both sexual cells.

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[20] PFEFFER, W., Plant physiology. Eng. ed. Vol. 1. pp. 199. 1899.

[21] DITTSCHLAG, E., Zur Kenntnis der Kernverhältnisse von *Puccinia Falcariae*. Centralbl. Bakt. II. **28**:473–492. *pls. 3. figs. 6.* 1910.

[22] HOFFMANN, H., Zur Entwicklungsgeschichte von *Endophyllum Sempervivi*. Centralbl. Bakt. **32**:137–158. *pls. 2. figs. 14.* 1911.

The life history of *Endophyllum Sempervivi* is peculiarly interesting because in that form the aecidiospores function as teleutospores. HOFFMANN finds that the binucleate basal cells arise from fusion of cells in the lower part of the aecidium. The axis of fusion, however, may lie in any direction, and there is no palisade-like arrangement of the fusion cells. The paired nuclei of the aecidiospore fuse and the subsequent processes are like those in teleutospores. The sporophyte phase is restricted to the aecidiospore mother cell and the two cells (aecidiospore and intermediate cell) formed from it.

In both of these forms the binucleate cells arise from the fusion of fertile cells, whose contiguous walls are dissolved. In this respect the process differs from the migration of nuclei through pores as described by BLACKMAN in his account of *Phragmidium violaceum*.

In a short note BEAUVERIE[23] reports further observations on the "corpuscules métachromatiques" which he finds in the mycelium of an unidentified rust of wheat and also in the host cells. The author now identifies these bodies with the "excretion bodies" of ZACH, and believes they remain in the host cells after the hyphae themselves have been digested.—H. HASSELBRING.

Embryo sac of Gunnera.—Ever since the investigation of *Gunnera* (Haloragidaceae) by SCHNEGG in 1902, the genus has been included with those interesting angiosperms (as *Peperomia*) displaying an excessive number of nuclei in the embryo sac preceding fertilization. It was very desirable to study the situation more critically, and this has been done by SAMUELS[24] for *G. macrophylla*. The sequence of events is as follows: The solitary hypodermal archesporial cell (mother cell) develops directly into the embryo sac, no tetrad in the ordinary sense being formed. At the first (heterotypic) division of its nucleus the reduced number of chromosomes was repeatedly observed to be 12. At the second division (four nuclei) two nuclei assume the micropylar polar position, and the other two are against the wall of the sac in the equatorial plane, and a little later move toward the antipodal pole. The polarity of the sac is thus attained at the 4-nucleate state. At this time the inner integument fuses to close the micropyle, and therefore the pollen tube was observed to pierce the integuments to reach the sac. The numerous vacuoles that appear during the second division fuse into a large central vacuole during the development of polarity. At the third division (eight nuclei) the upper one of the two micropylar nuclei divides to two nuclei side by side; and at the fourth division (16 nuclei) each of these two nuclei divides to two nuclei vertically placed. These four micropylar nuclei are the egg, the synergids, and the micropylar

[23] BEAUVERIE, J., La signification des corpuscules métachromatiques dans les cellules de céréales infestées par la rouille. Compt. Rend. Soc. Biol. **70**: 461–463. 1911.

[24] SAMUELS, J. A., Études sur le développement du sac embryonnaire et sur la fécondation du *Gunnera macrophylla* Bl. Archiv für Zellforsch. **8**: 53–120. *pls. 3–5. figs. 23.* 1912.

polar, not merely in position but also in function. The micropylar polar then fuses with the upper six nuclei toward the antipodal region, resulting in a fusion nucleus of seven nuclei; while the remaining six nuclei form the antipodal complex. The cells of this complex enlarge after the entrance of the tube, but after fertilization they degenerate.

Spermatogenesis was also followed, verifying the chromosome count, and showing a remarkable behavior of the pollen grain in frequently sending two tubes into the same style. Double fertilization was observed, so that the endosperm-forming nucleus finally becomes a fusion of eight cells.

SAMUELS discusses at length the relation of such a 16-nucleate embryo sac to the embryo sacs of gymnosperms. He also concludes that such a sac represents four megaspores in its origin.—J. M. C.

Paleobotanical notes.—In 1906 SCOTT published briefly the genus *Botrychioxylon*, and now there has appeared the full account.[25] The genus is of special interest in being a true fern (Botryopterideae) in which a stele of simple form "has advanced in the direction of substituting secondary for primary xylem." There is also anatomical evidence that it holds an intermediate position between Botryopterideae and Ophioglossaceae, thus linking the latter with the ancient ferns.

ARBER[26] has described a new species of the problematical genus *Psygmophyllum*, from the Lower Carboniferous of Newfoundland, and in a revision of the genus recognizes six species, distributed from Upper Devonian to Permian. As to the affinities of the genus, nothing can be determined in the absence of fructifications. There is a suggestive resemblance of the leaves to those of *Ginkgo*, but ARBER is convinced that the similarity is purely artificial. He associates the genus with other genera of the Paleozoic (as *Ginkgophyllum*, *Dicranophyllum*, etc.) as a distinct group under the name *Palaeophyllales*, which may or may not have been the ancestors of the Ginkgoales.

Dr. STOPES[27] has recorded the existence of angiosperms in the Aptian (Lower Cretaceous) of England, an earlier horizon than any in which angiosperms were known to occur. The specimens are in the collections of the British Museum of Natural History, and have been made the basis of the description of three new genera (*Aptiana*, *Woburnia*, *Sabulia*). The structure of the wood lends no support to the view that angiosperms arose from gymnosperms, since it is like that of high-grade angiosperms in all details. The wood

[25] SCOTT, D. H., On *Botrychioxylon paradoxum*, sp. nov., a paleozoic fern with secondary wood. Trans. Linn. Soc. London II. Bot. **7**:373–389. *pls. 37–41.* 1912.

[26] ARBER, E. A. NEWELL, On *Psygmophyllum majus*, sp. nov., from the Lower Carboniferous rocks of Newfoundland, together with a revision of the genus and remarks on its affinities. Trans. Linn. Soc. London II. Bot. **7**:391–407. *pls. 42–44. fig. 1.* 1912.

[27] STOPES, MARIE C., Petrifactions of the earliest European angiosperms. Phil. Trans. Roy. Soc. London B **203**:75–100. *pls. 6–8.* 1912.

does not occur in definite bundles, and the rays of *Aptiana* are multiseriate. The question of genetic connections must await further information, but the author well remarks that the chief importance of these three genera "is that they are so old, and that they prove the existence of undoubted higher woody angiosperms in Northern Europe at this time."—J. M. C.

The biology of Uredinales. An excellent summary of our knowledge of Uredinales is given by MAIRE.[28] Since the article is itself of the nature of a review, it needs to be mentioned here merely with reference to its scope, and to indicate new matter and views introduced by the author. The subject is treated under two heads: (1) the individual evolution and the sexuality of the Uredinales, and (2) the relation of the Uredinales to their hosts and to their environment.

The first part is chiefly an account of recent progress in the cytology of the rusts, with a brief exposition of the theories regarding their origin. The author himself believes the Uredinales and the higher Basidiomycetes to have had a common origin with the Ascomycetes. This view is based mainly on the presence of apparently functionless spermatia in the rusts and in some of the Ascomycetes, and on the existence of minute conidia possibly representing ancestral male cells among the Basidiomycetes.

In connection with the discussion of those rusts which have shortened life histories, the author introduces an amplification of SCHROETER'S classification of these forms. By taking into consideration all the spore forms, including the spermatia, he obtains the following biological groups: O-I-II-III, *eu*-Uredinales; I-II-III, *cata*-Uredinales; O-II-III, *brachy*-Uredinales; O-III, *hypo*-Uredinales; O-I-III, *opsi*-Uredinales; I-III, *catopsi*-Uredinales; II-III, *hemi*-Uredinales; II, *pyro*-Uredinales. Heteroecism and autoecism are expressed by the prefixes *hetero-* and *auto-* in the manner suggested by DUGGAR.

The second part takes up such more general phases of the work on biology of rusts as the types of development of the Uredinales, the rôle of the different spore forms, dissemination and infection, and the more theoretical questions relating to the host-relationships and the origin of species and of heteroecism within the group, and finally the various types of morphogenic changes induced by rusts in their hosts.—H. HASSELBRING.

The mistletoes.—At the April meeting of the National Academy of Sciences, Dr. TRELEASE presented a revision of *Phoradendron*. An abstract of his paper is as follows: There are distinguished 83 forms of this exclusively American genus of mistletoes on the mainland north of the Isthmus, of which 72 are regarded as species and the remaining 11 as varieties. About half of them are Mexican, one-fourth Central American, and one-fourth belong to the

[28] MAIRE, RENÉ, La biologie des Urédinales. Progressus Rei Bot. 4:110–162. 1911.

United States. Three main groups are recognized: one with very few-flowered spikes, growing on conifers, about equally divided between the United States and the Mexican highlands, comprising 12 species; one with more numerous flowers, growing on various angiosperms, comprising 11 United States and 18 Mexican species, also limited to the North; and one, differing from the second in the constant presence of scales at the base of at least its lowermost internodes, containing 14 Mexican and 17 Central American species. The first two groups are distinctly boreal and neither passes into the West Indies. The third group is distinctly equatorial, disappears well below the boundary between Mexico and the United States, and contains the exclusive representation of the genus in South America and the Antilles, more than half of its species occurring in this extralimital region. Except for two of these tropical species to which a wide range is ascribed, none occurs over so large an area as the common mistletoe of the eastern United States, which in distribution about coincides with the bald cypress.

A new aquatic fungus.—*Allomyces arbuscula*, a new generic type of the Leptomitaceae, has been described by BUTLER,[29] who found the fungus growing on dead flies in still water in Pusa and Poona, India. The individual plants consist of a basal cell which is attached to the fly by means of rhizoids, and at the apex branches more or less dichotomously to form a fan-shaped body of a few short cells. These give off slender branches which terminate either in zoosporangia or in sporangia containing a single thick-walled, brown resting spore. After the formation of a terminal sporangium, the axis is continued by a branch arising below the sporangium. Thus a sympodial system is built up as in *Phytophthora*. The fungus is peculiar in having a completely septate thallus, not usual among the Phycomycetes. The author regards it as a near ally to *Blastocladia* on account of the peculiar parthenogenetically developed oospores, which he suggests may have been derived from the *Monoblepharis* type through loss of the motile sperms.—H. HASSELBRING.

A bee hive fungus.—Miss BETTS[30] has described a new genus (*Pericystis alvei*) of "bee-hive fungus," which grows on pollen stored in the combs of the honey bee. The fungus is said to be "undoubtedly a normal inmate of the healthy bee-hive, and is, so far as is known, confined to that habitat."—J. M. C.

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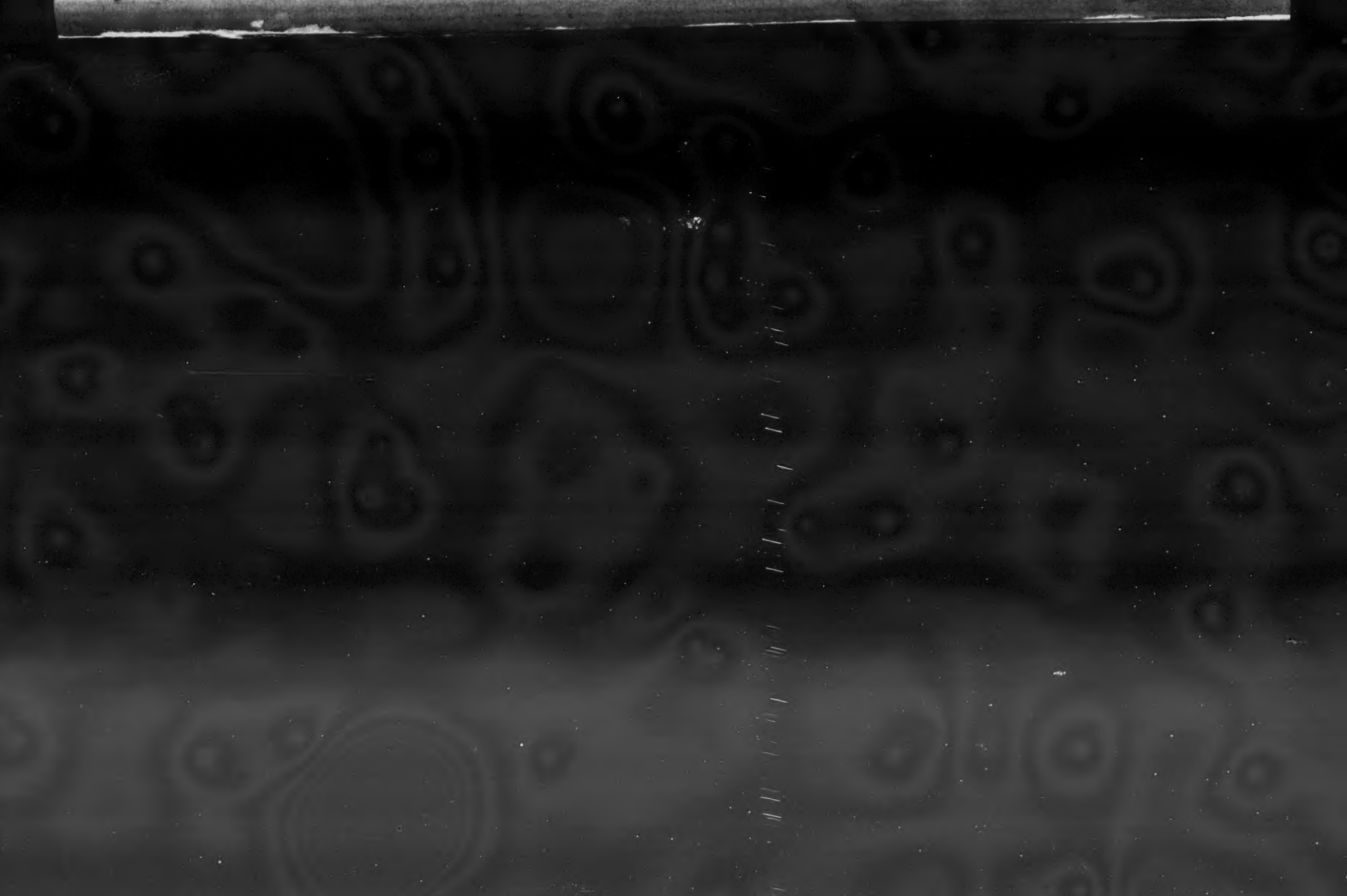
[29] BUTLER, E. J., On *Allomyces*, a new aquatic fungus. Ann. Botany **25**:1023–1035. *figs. 8.* 1911.

[30] BETTS, ANNIE D., A bee-hive fungus, *Pericystis alvei*, gen. et sp. nov. Ann. Botany **26**:795–799. *pls. 75, 76.* 1912.



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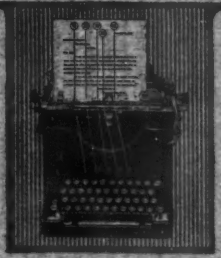

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